

# A PRELIMINARY SYNOPSIS OF SALPIGLOSSIS AND OTHER CESTREAE (SOLANACEAE)<sup>1,2</sup>

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## ABSTRACT

The genera *Browallia*, *Cestrum*, *Hunzikeria*, *Leptoglossis*, *Nicotiana*, *Nierembergia*, *Petunia*, *Reyesia*, and *Salpiglossis*, all members of the mainly Neotropical tribe Cestreae of the Solanaceae, are reviewed and generic lines are discussed. *Hunzikeria*, *Leptoglossis*, *Reyesia*, and *Salpiglossis* are given extensive attention, and a new species of *Hunzikeria* is described. *Bouchetia* is placed into synonymy under *Salpiglossis*. An evolutionary path from primitive ancestors to modern, advanced members of the group is postulated.

Several genera of Solanaceae in tribe Cestreae have long been subject to confusion, and this paper suggests resolution of some of the problems. The names *Bouchetia*, *Browallia*, *Cestrum*, *Hunzikeria*, *Leptoglossis*, *Nicotiana*, *Nierembergia*, *Petunia*, *Reyesia*, and *Salpiglossis* are reviewed. The plants are mostly herbs or diminutive shrubs, and they occur in North and South America, some genera being disjunct. Although the study has spanned five years, this paper must be regarded as a report of unconcluded work rather than a completed investigation. Few living plants were seen and the herbarium survey was not exhaustive. In particular, species limits require definition. As the early emphasis was on North American species, these species receive more detailed treatment than those of South America.

## CLASSIFICATION AND ORIGINS

Wettstein (1892, 1895) placed the genera discussed here into two tribes, the Cestreae and Salpiglossideae, separating the Salpiglossideae by their reduced number of stamens. Within the Cestreae, he recognized three subtribes: the Cestrinae with *Cestrum* and two discordant genera; the Goetzeinae, which is not solanaceous, and the Nicotianinae with *Nicotiana* and several of the genera discussed here. D'Arcy (in press) placed both tribes in subfamily Cestroideae. In the belief that *Cestrum*, *Nicotiana*, and *Salpiglossis* represent different levels of evolution within the same phylad and should not be separated into different tribes, Wettstein's subtribe Nicotianinae and tribe Salpiglossideae are here united into one tribe, Cestreae. Hunziker (1977) proposed the tribes Schwenkieae and Parabouchetieae for elements in subfamily Cestroideae which are distant from the pre-*Cestrum* ancestor of tribe Cestreae. Evidence has mounted (Gentry, in press) that the Australian elements of subfamily Cestroideae other than *Nicotiana* also have origins remote from the *Cestrum* ancestor and should be separated as tribe Anthoceraceae. With separation of these three tribes, most of the other genera of subfamily Cestroideae appear to form a natural unit, the tribe Cestreae, with

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the following genera: *Benthamiella*, *Browallia*, *Brunfelsia*, *Cestrum*, *Combera*, *Fabiana*, *Hunzikeria*, *Leptoglossis*, *Nicotiana*, *Nierembergia*, *Phrodus*, *Petunia*, *Reyesia*, *Salpiglossis*, *Sessea*, and *Streptosolen*. Some genera of subfamily Cestroideae are of uncertain placement, e.g., *Sclerophylax* (see Hunziker, 1977) and *Salpiglossis* (see Tucker, 1969).

#### FLORAL EVOLUTION

While there may be several explanations for the variation in floral morphology in genera of the group, D'Arcy (1975) suggested one explanation which he believed to be based on selective pressures by pollinators. This explanation postulated that starting with a campanulate corolla with stamens inserted low in the corolla tube and clustered loosely at the mouth as in *Petunia* or *Nicotiana* subgenus *Rustica*, there has been a tendency towards closure of the corolla mouth with compression of the anthers and stigma, and in some genera such as *Browallia* (Fig. 1A) or *Hunzikeria* (Fig. 1B), the corolla mouth is tightly plugged by stamens or stigma. Concurrent with this change in floral form have been tendencies for higher insertion of stamens, fusion of filaments, reduction of anthers, and elaboration of style. At this stage the stamens are didynamous and the corolla is irregular. Following this intermediate stage of small-mouthed corollas, further evolution appears to have taken place in two genera, *Nierembergia* and *Salpiglossis*. In *Nierembergia* (Fig. 1F), the anthers and stigma have become exerted from a narrow corolla mouth. The connation of filaments may have evolved before this exertion. In *Salpiglossis* (Fig. 1E), the corolla seems to have opened again, taking on a shape much like that of the unspecialized *Petunia*, with reduced stamen number and anther thecae, and a somewhat elaborated stigma remaining as evidence of earlier passage through the intermediate form just noted. Whether or not the genera are undergoing the exact evolutionary steps just outlined, it is plausible to classify the genera into several groups according to level of floral specialization (Table 1).

The above proposal can be examined in the light of trends within natural and extant genera. Within *Cestrum* (D'Arcy, 1973, 1975) there is a trend from the wide corollas and low stamen insertion of sect. *Habrothamnus* to narrow corollas with higher insertion in sect. *Cestrum*. In *Nicotiana* (Goodspeed, 1954) species in the more primitive subgenus *Rustica* have low stamen insertion and anthers and stigma loosely clustered at the corolla mouth, while in the more advanced subgenus *Petunioides* many species have high stamen insertion and the anthers and stigma are compressed at the mouth of salverform corollas. However, in members of subgenus *Nicotiana* (*Tabacum*), which is also a specialized group according to Goodspeed, stamen insertion has remained low while the stamens and style are long exerted from an open, asymmetrical corolla mouth; this flower corresponds in some ways to Stage III noted in Table 1, but it is uncertain whether this flower ever underwent an evolutionary Stage II. Thus within *Cestrum* and *Nicotiana* we can see trends corresponding to the three stages proposed above, but in subgenus *Nicotiana* current morphology suggests some different course of evolution. The pre-Cestroid ancestor postulated by Goodspeed may well have

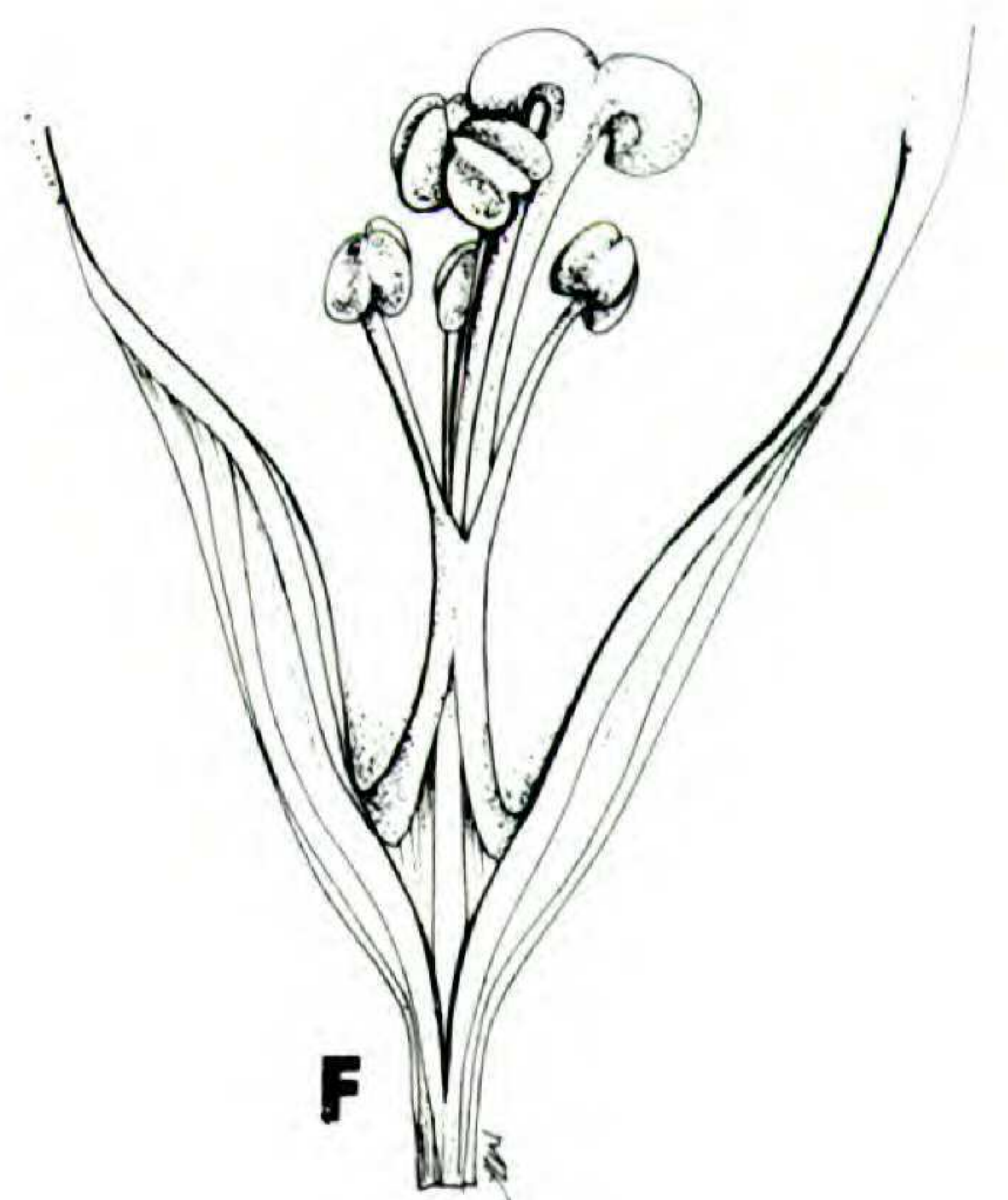
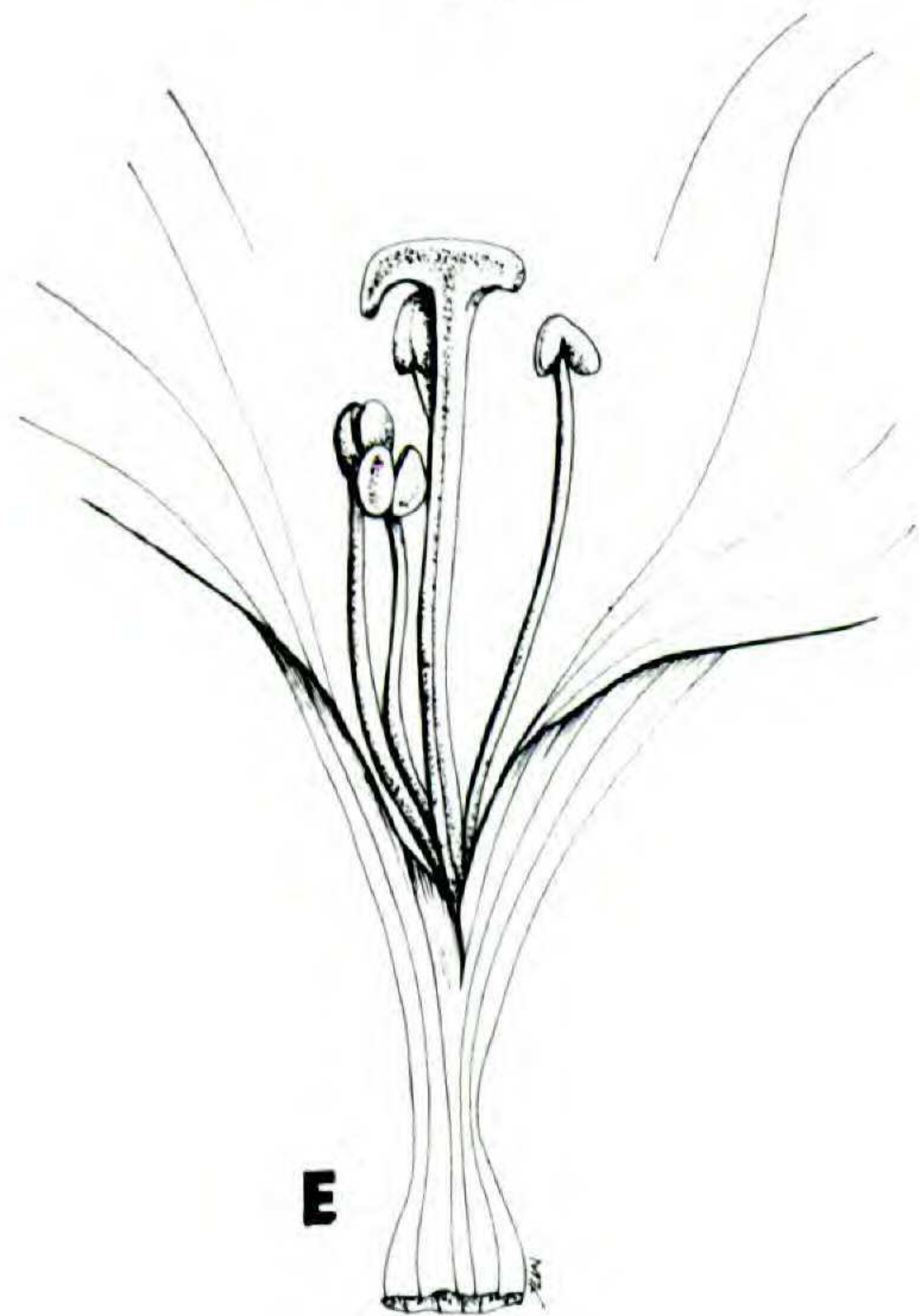
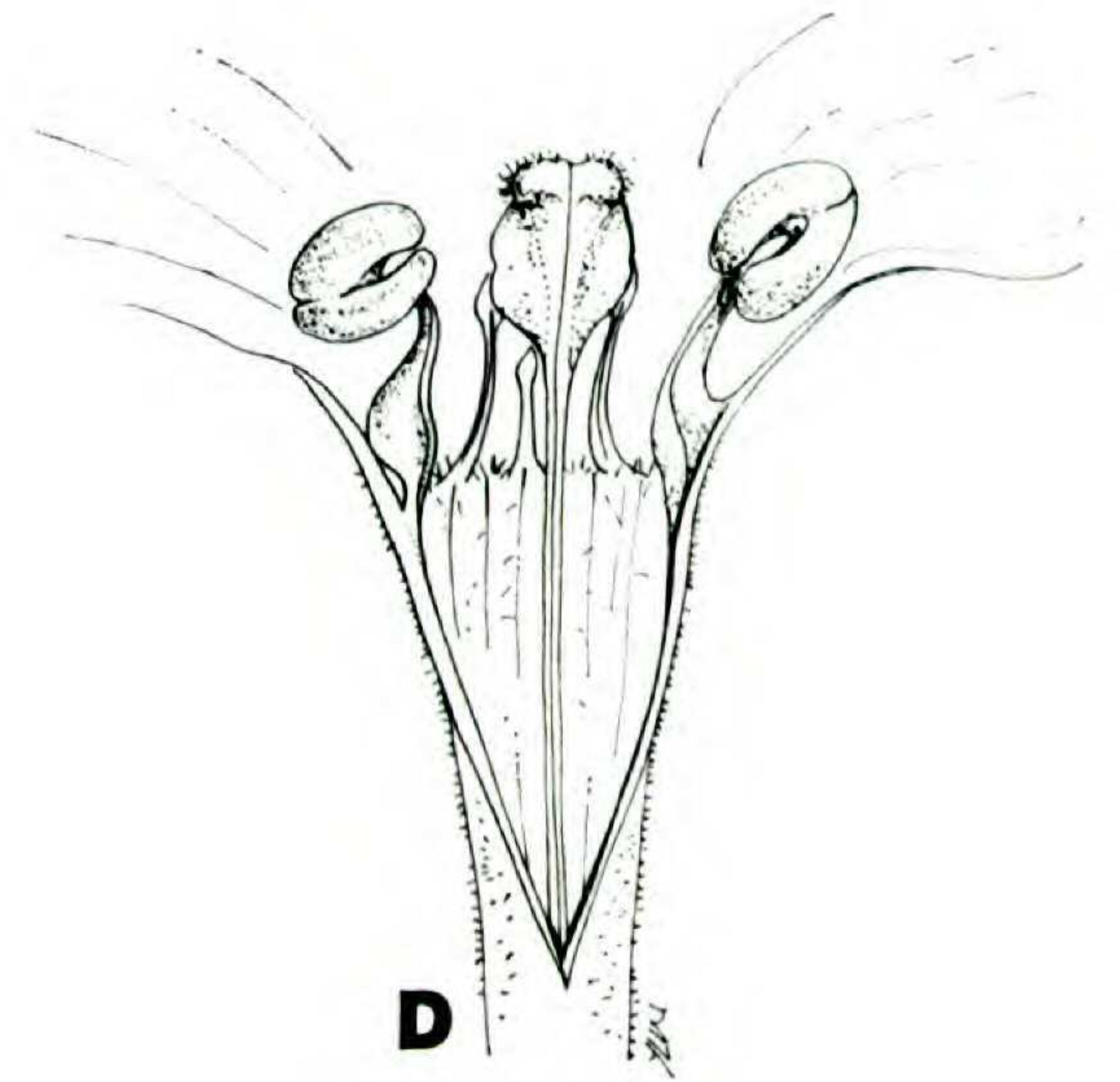
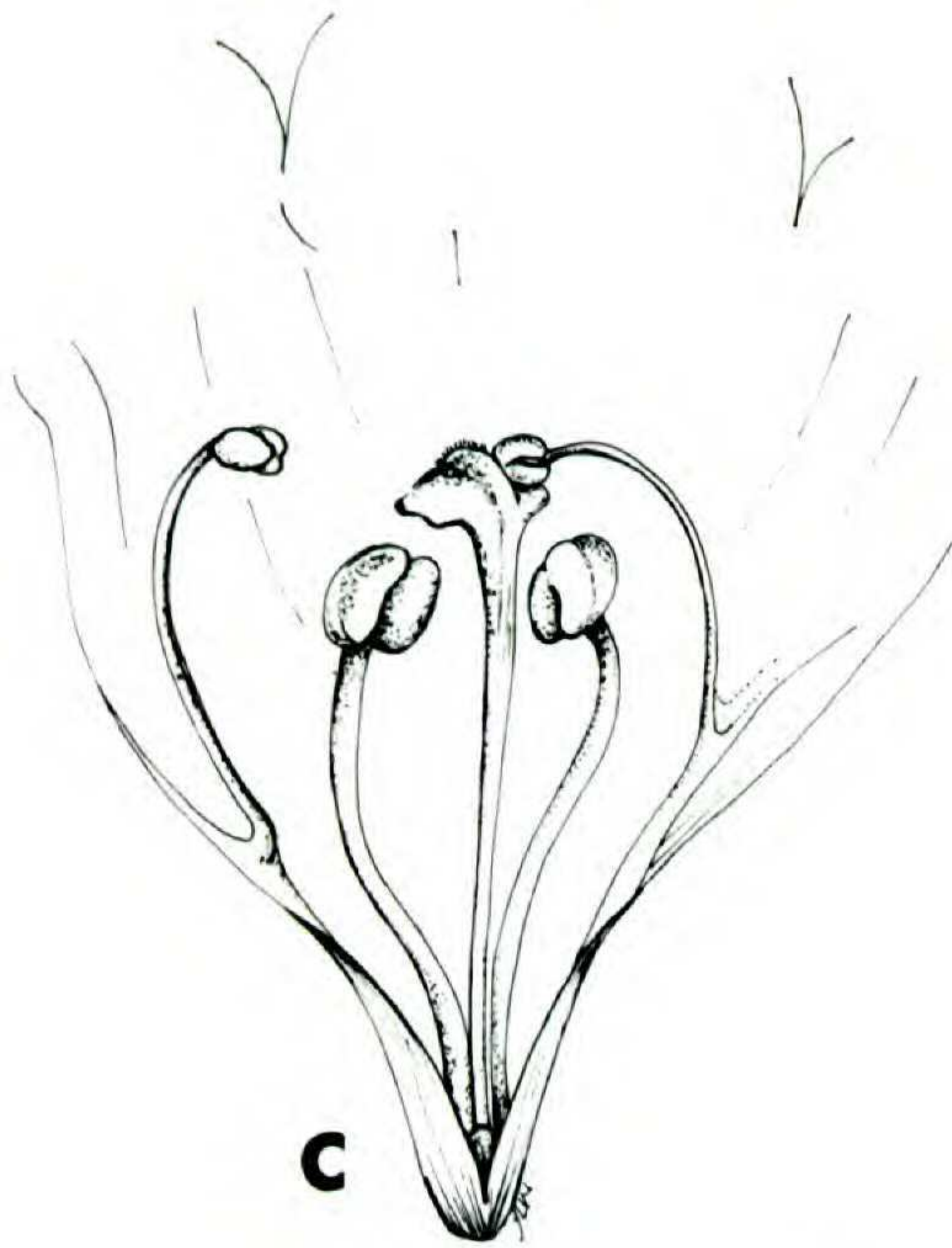
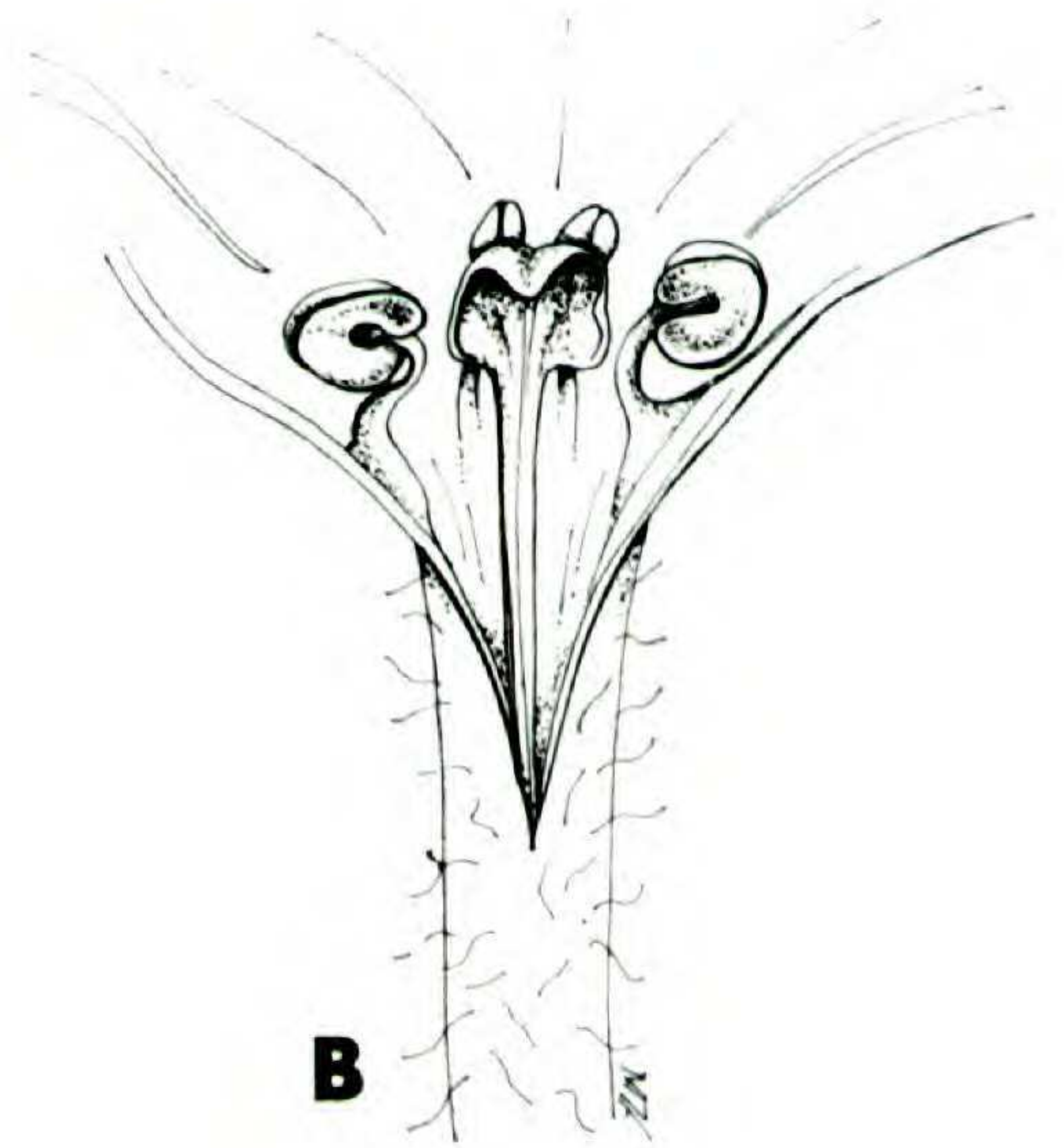
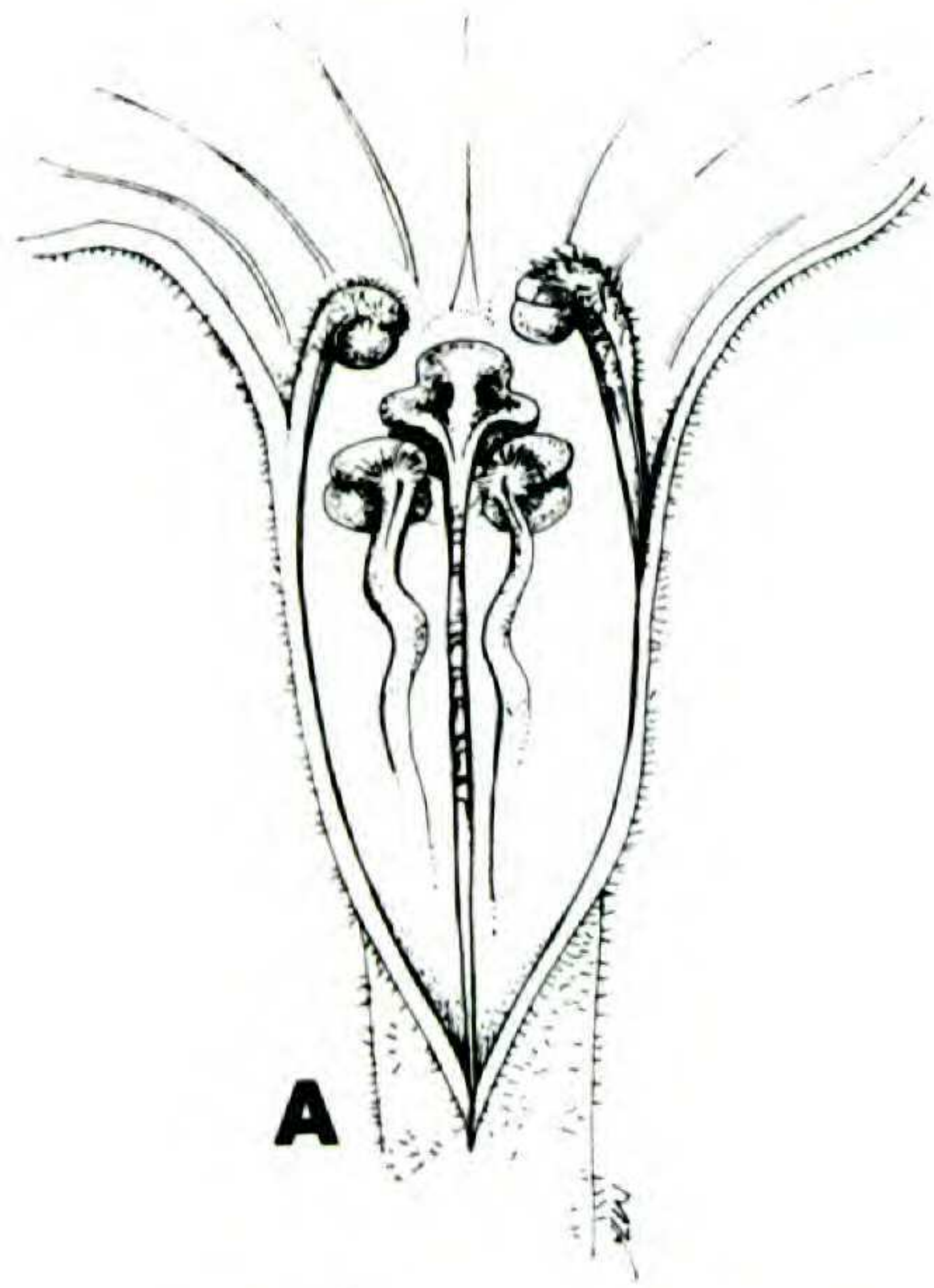


TABLE 1. Specialization in flowers in the Cestreae.

Stage	General	Floral characters
I	<i>Cestrum</i> (sect. <i>Habrothanmus</i> ) <i>Nicotiana</i> (subgen. <i>Rustica</i> ) <i>Petunia</i>	Corolla regular. Corolla mouth open, anthers and stigma clustered loosely. Stamens 5, alike, inserted low in the tube. Stigma small, capitate or 2-lobed.
II	<i>Browallia</i> <i>Cestrum</i> <sup>a</sup> (sect. <i>Cestrum</i> ) <i>Hunzikeria</i> <i>Leptoglossis</i> <i>Nicotiana</i> (subgen. <i>Petunioides</i> ) <sup>a</sup> <i>Reyesia</i>	Corolla zygomorphic. Corolla mouth narrow, anthers and stigma tightly packed. Stamens 4(5), didynamous, inserted high in the tube, some anthers reduced. Stigma elaborated, sometimes 2-armed.
III	<i>Nicotiana</i> (subgen. <i>Nicotiana</i> ) <sup>a</sup> <i>Nierembergia</i> <i>Salpiglossis</i>	Corolla slightly zygomorphic. Corolla mouth open, anthers and stigma clustered loosely or exserted. Stamens 4(5), inserted low in the tube, some anthers reduced. Stigma elaborated.

<sup>a</sup> Group does not have all characters of this stage.

had flowers somewhat like those of Stage I. Whether the genera with Stage II or Stage III were all derived directly from Stage I or pre-Stage I ancestors or whether they arose sequentially is not clear. But it is quite artificial to associate genera in the tribe which have undergone stamen reduction, as such genera now represent endpoints in discrete lines of evolution, some of them perhaps of considerable antiquity and stemming directly from primitive stocks.

#### DISTRIBUTION AND DISJUNCTION

Tribe Cestreae includes about 500 species in 15 genera occurring in North and South America, Australia, and Africa (Table 2). The greatest proportion of

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FIGURE 1. Floral evolution in the Cestreae, all views slightly exploded.—A–D. Stage II, the anthers and stigma fitting tightly to close the constricted corolla mouth.—A. *Browallia americana* L. Only the pubescent filament apices are visible from the outside ( $\times 5$ ). [After Gentry 4459 (OKLA).]—B. *Hunzikeria texana* (Torr.) D'Arcy. Only the apical rim of the stigma is visible from the outside. The basal portion of the stigma has been referred to as wings ( $\times 10$ ). [After Wynd & Mueller 140 (MO).]—C. *Leptoglossis linifolia* (Miers) Griseb. Only the apex of the stigma is visible from the outside. A staminode is present. The basal portion of the stigma has been referred to as wings ( $\times 8$ ). [After O. Kuntze 16 Jan. 1892 (NY).]—D. *Reyesia chilensis* Clos. Because the flower is so small, the anthers and stigma are tightly appressed, although there is no constriction of the corolla tube. The stamens are clearly didynamous. [After Werdermann 156 (MO).]—E–F. Stage III, evolution beyond the levels of the other genera.—E. *Salpiglossis erecta* (Dun.) D'Arcy. The stamens are only 4 and the anthers are somewhat unequal in size. The style has definite arms. ( $\times 6$ ). [After Lindheimer 471 (MO).]

TABLE 2. Distribution of the Cestreae.

Genera	N. America Mainly temperate	S. America Mainly temperate	American Mainly tropical <sup>a</sup>	Other (Australia, Africa)
<i>Benthamiella</i>	—	10	—	—
<i>Browallia</i>	—	—	2	—
<i>Brunfelsia</i>	—	—	25	—
<i>Cestrum</i>	few	few	175	?
<i>Combera</i>	—	2	—	—
<i>Fabiana</i>	—	25	—	—
<i>Hunzikeria</i>	2	—	1	—
<i>Leptoglossis</i>	—	3	—	—
<i>Nicotiana</i>	9	30	—	21
<i>Nierembergia</i>	1	35	—	—
<i>Petunia</i>	1	40	2	—
<i>Reyesia</i>	—	5	—	—
<i>Salpiglossis</i>	2	3	—	—
<i>Sessea</i>	—	—	5	—
<i>Streptosolen</i>	—	—	1	—
Total	ca. 18	ca. 155	211	21

<sup>a</sup> Does not include upland Peru, Ecuador, Mexico, Guatemala.

species is of the New World, only about 21 species of *Nicotiana* occur in Australia and 1 species in South West Africa. The greatest diversity is in South America where 14 genera occur, 5 of them endemic. Eight genera occur in North America, none of them endemic. In total species the tribe is about equally tropical and temperate, but in genera the tropics are poorly endowed, only 6 genera occurring there and only 4 of these endemic. The majority of tropical species are in the widespread genus *Cestrum*, which has a few species ranging into the temperate zones. D'Arcy (1973, 1975) noted that the most primitive members of *Cestrum* sect. *Habrothamnus* occur in Mexico.

Four genera are disjunct between North and South America with no species native in the intervening tropical regions of Central America, Colombia, or lowland Peru and Ecuador. *Nicotiana*, *Nierembergia*, *Petunia*, and *Salpiglossis* have the majority of their species in South America with a minority of species disjunct northward. The several workers, e.g., Raven (1962, 1963) and Solbrig (1972) who have written about North-South American disjunctions have not noted the disjunction in this group. None of these plants has fruits adapted for ingestion by birds; they all have minute seeds in dry capsules. Such seeds might be transported on the feet of birds. In some cases the species are little different from their disjunct counterparts, but in other cases there has been substantial divergence. For example, in *Nicotiana*, sects. *Bigelovianae*, *Nudicaulis* and *Trigonophyllae* of subgenus *Petunioides* are endemic in North America. The most primitive subgenus, *Rustica*, is endemic to South America. Because there is endemism at several levels on both continents, it is likely that stocks have moved at different times over long periods of time. South America would appear to be the ancestral region for the Cestreae, as here is where the greatest generic diversity occurs, and in South America there is also diversity in other subfamilies in the Solanaceae.

## REVIEW OF GENERA

The following review discusses genera in the order of floral specialization suggested in Table 1. North American groups are more fully treated than those of South America, and for some of the large genera, only the species of North America are noted in detail. Besides the genera noted here, the Cestreae embraces *Brunfelsia* of lowland tropical America and six other genera endemic to South America: *Benthamiella*, *Combera*, *Fabiana*, *Phrodus*, *Sessea*, and *Streptosolen* (see Table 2). Keys separating most of the genera were presented by Wettstein (1895), Bentham & Hooker (1876), and Millán (1931). The following key notes differences believed to be diagnostic.

- a. Corolla mouth open, the anthers and stigma clustered loosely at the mouth; stamens inserted low in the tube.
  - b. Stamens 5, all thecae alike; stigma minute, obscurely 2-lobed.
    - c. Fruit a berry; plants mostly woody ..... 1. *Cestrum*
    - cc. Fruit a dry capsule; plants mostly herbaceous.
      - d. Flowers solitary; upper leaves appearing opposite ..... 3. *Petunia*
      - dd. Flowers in inflorescences; all leaves alternate ..... 2. *Nicotiana*
  - bb. Stamens 4(5), usually some thecae reduced; stigma elaborated, 2-armed or lamellar.
    - e. Stamens often unequal but not in pairs ..... 9. *Salpiglossis*
    - ee. Stamens clearly didynamous ..... 7. *Reyesia*
- aa. Corolla mouth narrow, mostly plugged by the anthers and style; stamens inserted high in the tube.
  - f. Stamens and style exerted; filaments partly connate ..... 8. *Nierembergia*
  - ff. Stamens and style included or only minutely exerted; filaments free.
    - g. Stamens 4, didynamous; fruit a capsule.
      - h. Corolla cylindrical with a small limb; calyx narrow ..... 6. *Leptoglossis*
      - hh. Corolla salverform with a large limb; calyx mostly broad.
        - i. Corolla mouth closed by expanded filament apices; seeds numerous, less than 1 mm across, prismatic and evenly pitted ..... 4. *Browallia*
        - ii. Corolla mouth closed by stigma; seeds few, more than 1 mm across, rounded and coarsely sulcate ..... 5. *Hunzikeria*
    - gg. Stamens 5, often unequal but not in pairs; fruit a berry ..... 1. *Cestrum*

1. *Cestrum* L., Sp. Pl. 191. 1753; Gen. Pl., ed. 5. 88. 1754. TYPE: *C. nocturnum* L.

*Cestrum*, the largest genus in the tribe, is predominately tropical in distribution but several species range south as far as Chile and Uruguay and several range north as far as the southern United States and the Bahamas. Two sections are recognized, sect. *Habrothamnus* with about 30 species in eastern Mexico and ranging into Central America, and sect. *Cestrum* comprising the rest of the species. D'Arcy (1973, 1975) has postulated that sect. *Habrothamnus* is primitive. In this section, species have the most varied floral morphology, the calyx is larger, the corollas are larger and inflated, the anthers are longer, the stamens are inserted lower in the tube, the ovules are numerous, and the endosperm is distinctively colored (Francey, 1935). *Cestrum* is seemingly primitive in the tribe, and its immediate precursors may have been ancestral to some other genera in the tribe.

2. *Nicotiana* L., Sp. Pl. 180-1. 1753; Gen. Pl., ed. 5. 84. 1754. TYPE: *N. tabacum* L.

*Nicotiana* is a large genus with centers in Andean South America, Mexico, and Australia. The genus was monographed by Goodspeed (1954) and the Australian species were revised by Burbidge (1960). Goodspeed recognized three subgenera, the two most primitive, *Rustica* and *Nicotiana* being confined to western South America, and the most advanced, *Petunioides*, with representatives in North and South America and in Australia. Flowers of subgenus *Nicotiana* do not seem to have followed the pathway in floral evolution postulated for other genera discussed here. Some members of subgenus *Petunioides* of South America somewhat resemble *Leptoglossis*, especially in corolla shape, but the anthers are all alike, and while the filaments are sometimes unequal, they are not didynamous. Species of *Nicotiana* usually have a distinct throat between the tube and the limb, and this is not developed in either *Salpiglossis* or *Reyesia*. It is present in *Hunzikeria* and in *Leptoglossis*.

3. **Petunia** Juss., Ann. Mus. Natl. Hist. Nat. 2: 215, *tab. 47*. 1803. TYPE: *P. parviflora* Juss.

*Petunia* was revised by Fries (1911), who showed that it embraces about 40 species mainly of southeast Brasil with 1 species disjunct in North America. This disjunct species, *P. parviflora* Juss. also occurs in South America. It is the only species commented upon here.

In his monograph of *Nicotiana*, Goodspeed (1954) noted probable origins of *Petunia*, *Cestrum* and *Nicotiana*, suggesting that *Petunia* evolved from the most advanced ancestor of the group. Flowers of the widely cultivated *P. violacea* Lindl. resemble *Salpiglossis sinuata* Ruiz & Pavón discussed below but differ in having 5 perfect stamens and a small, unelaborated stigma.

- 3a. **Petunia parviflora** Juss., Ann. Mus. Natl. Hist. Nat. 2: 215, *tab. 47*. 1803. TYPE: Brasil, *Commerson* (P, not seen).

This species is unlikely to be confused with any others discussed here, for it has very leafy diffuse branches with the short, narrow leaves appearing to arise in fascicles. The tiny corollas are often concealed in the foliage and calyces. The stamens are alike although 2 anthers may be larger than the other 3. The stigma is 2-cleft as in other species of the genus, but it also tends to be radially broadened displaying a somewhat 2-armed appearance.

*Petunia parviflora* has a very wide, disjunct range, occurring in eastern warm temperate South America and in Mexico and the southern United States. A paludal weed, the seeds may be dispersed by mud on the feet of birds.

Because this species is well represented in many herbaria, usually correctly identified, no specimens are cited here.

4. **Browallia** L., Sp. Pl. 631. 1753; Gen. Pl., ed. 5. 278. 1754. TYPE: *B. americana* L.

*Browallia* is one of the few zygomorphic members of the Cestreae which is tropical in distribution. Nomenclature and other features of the genus were surveyed by D'Arcy (1973). In *Browallia*, the stamens are didynamous, the upper

pair much larger, and the corolla mouth is closed by broadly expanded, ciliate filament apices.

There are two species:

- 4a. **Browallia americana** L., Sp. Pl. 631. 1753. TYPE: Hort. Cliff. (BM, not seen, the original seed source was Panama [Miller, 1768, 'Browallia']).—FIG. 1A.
- 4b. **Browallia speciosa** Hook., Bot. Mag. tab. 4339. 1947. TYPE: not seen.
5. **Hunzikeria** D'Arcy, Phytologia 24: 283. 1977. TYPE: *H. texana* (Torr.) D'Arcy.

This genus embraces plants of Texas and Mexico which have been known as *Leptoglossis*. A most unusual feature of *Hunzikeria* is the seed (Fig. 2B). Only about 5 seeds are present per capsule and they are 1.5 mm long, much larger than in most other zygomorphic Cestreae. They are ellipsoidal or subreniform, cuneiform along one side and with about 8 transverse sulci and rounded ridges. The corolla is much like that of a *Nierembergia* with which plants have been confused in the past. The calyx, androecium, and seed are quite distinct from *Nierembergia*. Impressed by details of the androecia, Gray (1877) allied these plants with *Leptoglossis schwenkioides* of Peru (see below), but *Hunzikeria* differs from *Leptoglossis* in many features. Notable are the pedicels which are subtended by normal leaves or lack bracts altogether, the 5 short, deltoid calyx lobes, the obconical calyx tube, the filiform, long-exserted corolla tube, the broad rotate limb, and the capsule included in the calyx tube. The seeds plus the salverform corolla and obconical calyx distinguish *Hunzikeria* from other genera of Solanaceae. It is interesting that somewhat similar, radially sulcate seeds are found in *Solanum lumholtziana* Bartlett, a species of northwestern Mexico (Whalen, 1977). This is a striking convergence of seed morphology in plants from different subfamilies.

- 5a. **Hunzikeria coulteri** (A. Gray) D'Arcy, comb. nov.—FIG. 2C.

*Leptoglossis coulteri* A. Gray, Proc. Amer. Acad. Arts 12: 165. 1877. TYPE: Mexico, Hidalgo, Zimapán, Coulter 1346 (GH, not seen; K, duplicate).

*Nierembergia coulteri* (A. Gray) Hemsley, Biol. Cent.-Amer. 2: 437. 1882.

Whether *Hunzikeria coulteri* is taxonomically distinct from *H. texana* is uncertain. It is known to me only by the type; all other material I have seen with this determination has turned out to be *Salpiglossis*. The type collection was taken somewhat south of the apparent limits of *H. texana*. It is a more open, weaker plant with longer corolla tubes and perhaps slightly larger limb. The flowers may have been white. The calyces differ in that the intermediate vein to the sinuses divides below the middle and becomes 2 distinct veins distally. In all material seen of *H. texana*, this intermediate vein remains unified, at least until the upper  $\frac{3}{4}$  of the calyx tube. The calyx lobes of *H. texana* appear to be relatively shorter.



MEXICO. Hidalgo: Zimapán, *Coulter 1346* (K).

5b. *Hunzikeria steyermarkiana* D'Arcy,<sup>4</sup> sp. nov. TYPE: Venezuela, *Pittier 6419* (NY, holotype).

*Herb* to ca. 20 cm tall; roots short; stems terete, slender, puberulent with short, weak, curved hairs, perhaps glandular. *Leaves* obovate, to 4 cm long, 13 mm wide, apically obtuse, basally narrowed into an elongate, narrowly winged petiole, the midvein evident with ca. 3 nerves on each side, above sparingly short-glandular pubescent, glabrate beneath, manifestly ciliate; petiole 5–15 mm long, winged upwards, keeled at the base. *Inflorescences* solitary flowers at the tips of branches; pedicels glandular tomentose, slightly angled, ca. 3 mm long, becoming 5–7 mm long in fruit; bracts wanting. *Flowers* apparently held erect; calyx campanulate to obconical, 5-lobed, ca. 4 mm across, 5 mm long, slightly longer in fruit, glandular pilose outside, the tube 10-nerved, the lobes obtuse or deltoid, glabrate within; corolla salverform, drying mauve, the tube slender, to 10 mm long, exerted from the calyx, puberulent outside, longitudinally nerved, the limb rotate, to 15 mm across; stamens 4, didynamous, the anthers all alike, fertile; style apically winged, the stigma flat, cordate or rectangular, with 4 shallow grooves to accommodate the upper and lower anthers. *Capsule* included in the calyx.

This species differs from *H. texana* in its smaller corollas with shorter, relatively broader tubes, and in having all anthers alike, not reduced. The foliage is glabrate except on the margins, whereas in *H. texana* leaves are pubescent all over.

*Hunzikeria steyermarkiana* is known only from the subdesert area of Venezuela near the Caribbean coast just west of Caracas. It is named in honor of Julian Alfred Steyermark, an outstanding student of the Venezuelan flora.

VENEZUELA. CARABOBO: El Palito near Puerto Cabello in the cactus formation, 0–30 m, *Pittier 6419* (NY). Guaremales, road from Puerto Cabello to San Felipe in forest, 0–100 m, *Pittier 8882* (GH, NY).

5c. *Hunzikeria texana* (Torr.) D'Arcy, *Phytologia* 34: 283. 1977.—FIGS. 1B, 2A, 2B.

*Browallia* (*Leptoglossis*) *texana* Torr., U.S. & Mexican Boundary 2(1): 156. 1859. LECTOTYPE: Texas, *Wright 535* (NY; BM, F, G, MO, NY, P, TEX, isolectotypes).

*Nierembergia* (*Leptoglossis*) *viscosa* Torr., U.S. & Mexican Boundary 2(1): 155. 1859. LECTOTYPE: Texas, *Wright 535* (NY; BM, F, G, MO, NY, P, TEX, isolectotypes).

*Leptoglossis viscosa* (Torr.) Millán, *Darwiniana* 5: 489. 1941.

Diminutive woody *perennials* to 20 cm tall, branching from a woody base; stems slender but soon woody, viscid pilose with dense short hairs. *Leaves* entire, obovate to oblanceolate, occasionally cuneate, mostly 10–20 mm long, 5–8 mm wide, apically obtuse or sometimes acute, basally acute or acuminate, the venation obscure, viscid pilose, slightly more so beneath, the margins and costas ciliolate; petiole mostly 2–5 mm long. *Inflorescences* solitary or paired terminal or sub-

<sup>4</sup> *Hunzikeria steyermarkiana* D'Arcy, sp. nov. *Herba* parva, pubescens, glandulosa. *Folia* petiolata, ciliata, laminis glabris. *Flos* salverformis, staminibus quattuor, didynamis, antheris aequalibus, fertilis.

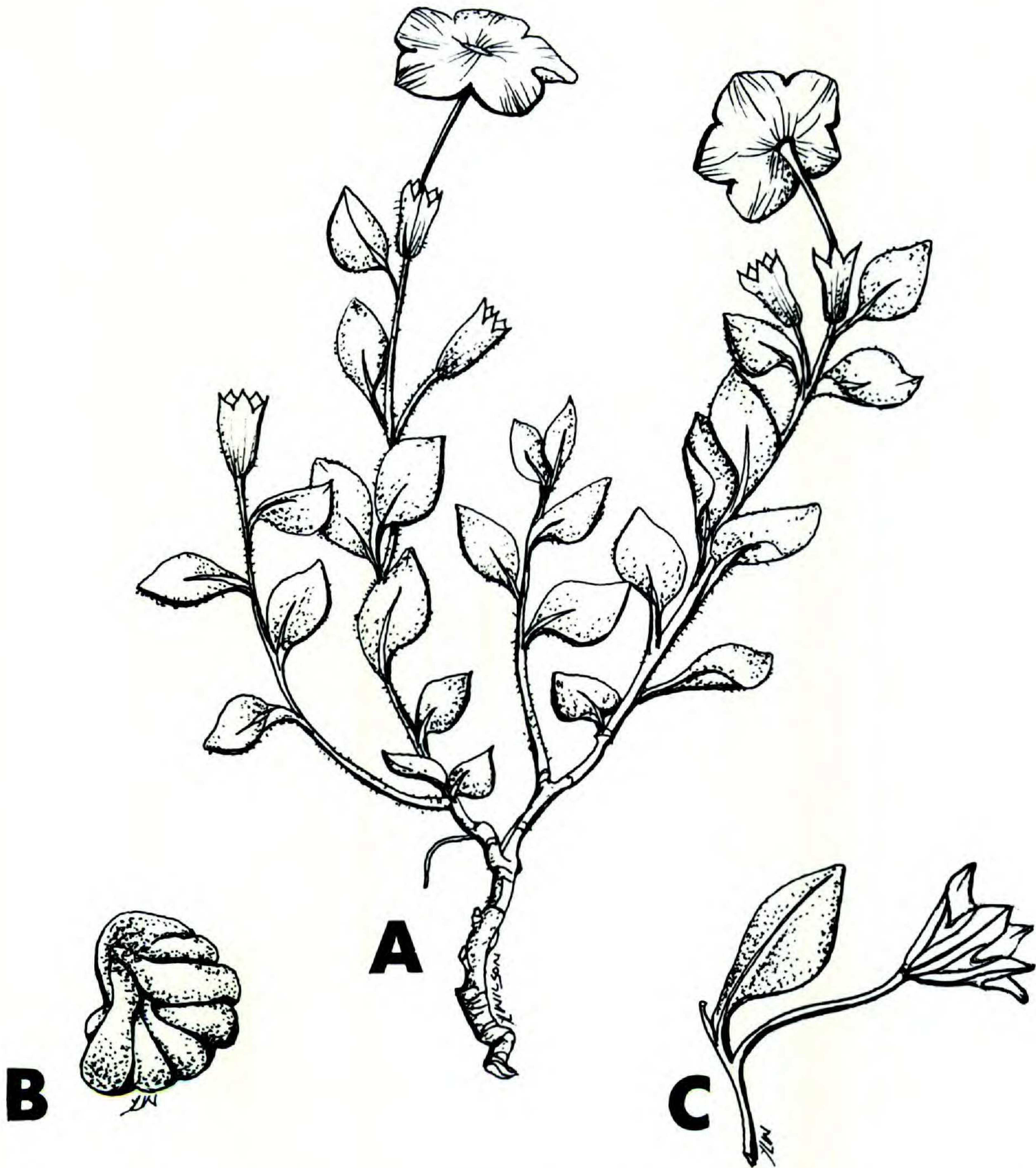


FIGURE 2. *Hunzikeria*.—A–B. *H. texana* (Torr.) D'Arcy.—A. Habit ( $\times 1$ ). [After Purpus 1911 (MO).]—B. Seed ( $\times 20$ ). [After Ripley & Barnaby 4183 (NY).]—C. *H. coulteri* (A. Gray) D'Arcy. Fruiting calyx ( $\times 1\frac{1}{2}$ ). [After Coulter 1340 (K).]

terminal flowers; pedicels terete, ca. 7 mm long, pilose, not accrescent, subtended by normal size leaves. *Flowers* with the calyx obconical, ca. 10 mm long, 10-nerved, pilose overall, scarcely accrescent, 5-lobed, the lobes deltoid, ca. 3 mm long; corolla "light-purple or purple-pink," salverform, pubescent outside with reduced hairs, the tube slender, 15–25 mm long, ca. 0.5 mm wide, scarcely expanded upwards, longitudinally nervate, the throat expanded around the anthers, ca. 2 mm long, the limb rotate, 20–23 mm across, slightly oblique on the tube, 5-lobed ca. halfway down, the lobes nearly regular, rounded-obtuse, the mouth tightly constricted around the stamens; stamens 4, the filaments inserted low in

the tube, the upper (ventral) pair of anthers much reduced, situated slightly above the lower pair, a filiform staminode sometimes present; style 2-winged just below the stigma, the stigma crescentic-2-armed, included and compressed by the anthers. *Capsule* included in the calyx tube, "2-valved," ca. 5 seeded, the seeds large, ca. 1.5 mm long, oblong, with ca. 8 coarse, transverse furrows, reddish, the furrows darker than the ridges.

The pubescence of this species consists of short, slender, uniseriate hairs 2–3 cells long. The basal cell is much broader than those above, and the apical cell usually oozes a small drop of sticky fluid. Some details of the above description were taken from Correll (1970).

Correll and various collectors' notes indicate that this species grows mainly on rocky, limestone slopes and ranges along the eastern side of the Edwards Plateau and the Sierra Madre Oriental. The Schott collection from Chihuahua is well to the west of this upland, and the type collection of *H. coulteri* (see above) is both south and west of it. Correll indicated that the species flowers from May to June in Texas; in Mexico, flowering collections have been taken in nearly every month of the year.

UNITED STATES. TEXAS: Devil's River, *Bigelow* (NY). Kinney Co., Anacacho Ranch, Anacacho Mountains, *Correll & Rollins* 32549 (TEX). 30 airline mi N of Del Rio, *Cory* 41529 (TEX). Valverde Co., Pecos River below bridge on Highway 90, 1200 ft, *Hinckley & Hinckley* 413 (TEX, US). Valverde Co., Devil's Lake, ca. 20 mi NNW of Del Rio, *McVaugh* 7733 (F, TEX). West Texas, *Neally* 1890 (F). Valverde Co., Devil's River, *Orcutt* 6036 (MO). Valley of Rio Grande near Donana, *Parry et al.* 630 (NY). Valverde Co., 3 mi E of mouth of Pecos River, *Ripley & Barnaby* 4183 (NY). On Bravo del Norte, *Schott* 1852 (F). Without locality, *Thurber* 1850–52 (F). Del Rio, *Whitehouse* 4/1/33 (TEX). Expedition from western Texas to El Paso, New Mexico, *Wright* 535 (BM, F, G, MO, NY, P, TEX).

MEXICO. CHIHUAHUA: *Schott* (F). COAHUILA: 2 km SW of Rancho San Miguel WSW of Ciudad Acuna, *Chiang et al.* 7502 (TEX). Saltillo-Piedras Negras road, *Crockett* 8125, 8129 (both TEX). Sierra de la Rata, 550–1700 m, *Johnston et al.* 10160F (TEX). 1 km N of Rancho de la Gavia on N side of Sierra de la Gavia, 1200 m, *Johnston et al.* 10276A, 10277 (both TEX). Cañon Bonanza, SE end of Sierra de la Purisima, 1300–1650 m, *Johnston et al.* 10296A (TEX). Muzquiz, *Marsh* 133 (TEX), 1046, 2110 (both F, TEX). Sierra de Gloria near Monclova, *Ripley & Barnaby* 14215 (NY). NUEVO LEÓN: 5 mi S of Monterrey, *Barkley et al.* 16M367 (TEX). Chipinque, *Barkley et al.* 7153 (TEX). Monterrey, *Edwards & Eaton* 1846 (NY). Punta de la Loma, 1700 m, *Etchison* 19 (TEX). Monterrey, 1800 ft, *Fischer* 26 July 1926 (TEX). Near Monterrey, *Johnston & Barkley* 16057M (F, MO, TEX). Road to Chipinque Mesa S of Monterrey, 2000 ft, *Johnston & Crutchfield* 5298 (TEX). Monterrey river valley, *Kenoyer* 18 Sept. 1937 (MO). Monterrey, *Kenoyer* 1142 (F, MO); *Lacas* 41 (F). Diente Canyon, near Monterrey, *Mueller & Mueller* 176 (F). Opposite mouth of Diente Canyon, *Muller* 2695 (TEX). Near Monterrey, *Pringle* 1924 (BM, F, MO, MPU, NY, P), 2687 (F). 3 mi W of Monterrey, *Rollins & Tryon* 5881 (TEX). Monterrey, *Smith* M134, M202 (both TEX); *Webster & Aguirre* 2955 (TEX). SAN LUIS POTOSÍ: N of Minas de San Rafael, *Chiang et al.* 8172 (TEX). Minas de San Rafael, *Purpus* 5012 (BM, F, MO, NY). TAMAULIPAS: Cañon de la Tamaulipeca, San Miguel, *Bartlett* 10650 (TEX). 6 mi N of Santander Jiménez, 800 ft, *Johnston* 4897 (TEX). 4 mi S of San Carlos on road to Padilla, *Johnston & Crutchfield* 4998B (TEX). Los Coyotes, *LeSueur* 628 (F, TEX). Matamoros-Victoria Highway, *Richardson* 1417 (TEX). Sierra between Jaumave and Victoria, *Rozynski* 157, 477 (both F).

6. **Leptoglossis** Benth., Bot. Voy. Sulphur 143. 1844. TYPE: *L. schwenckioides* Benth., non *Leptoglossum* Karsten (1879, fungi).

*Cyclostigma* Phil., Sert. Mendoc. Alt. 39. 1871. TYPE: *C. tenue* Phil., non *Cyclostigma* Hochst. ex Endl. 1842 (Apocynaceae), nec Klotsch in Seem., 1853 (Euphorbiaceae).

*Leptofeddea* Diels, Repert. Spec. Nov. Regni Veg. 16: 193. 1919. TYPE: *L. lomana* Diels.

The name *Leptoglossis* should apply only to three (perhaps more) species of western South America. Plants of North America formerly known as *Leptoglossis* are referred to *Hunzikeria*. In *Leptoglossis* the stamens are didynamous, much as in *Browallia* and *Hunzikeria*, but the corolla tube is usually broadly cylindrical with a small limb, and the calyx is narrow with conspicuously differentiated ribs. The stigma is elaborated and compressed, much as in the related genus *Brunfelsia*. The seeds are numerous, prismatic and finely tuberculate. The glandular-pubescent plants range from diminutive ephemerals to shrubs attaining a meter in height. The flowers are solitary or aggregated into ill-defined racemes or panicles, each flower subtended by a bract. *Leptoglossis* appears to be closely related to *Reyesia*, particularly to *R. cactorum* which occurs in the same part of South America. *Leptoglossis* was placed in synonymy under *Salpiglossis* by Wettstein (1895) but this is unjustified, as is placement of one species in *Schwenckia* by Grisebach. Alignment of *L. schwenkioides* with the two species below is provisional: they may be generically distinct.

6a. ***Leptoglossis linifolia*** (Miers) Griseb., Symb. fl. Argent. 241. 1879. (Transfer incorrectly attributed to Bentham & Hooker by Jackson, Index Kewensis 2: 63. 1894 [1895.])—FIG. 1C.

*Nierembergia linifolia* Miers, London J. Bot. 5: 174. 1846; Ill. S. Amer. Pl. 1: 98, tab. 20, fig. 1. 1850. LECTOTYPE: Argentina, Gillies 835 (K).

*N. linifolia* var. *macrophylla* Dun. in DC., Prodr. 13(1): 587. 1852. TYPE: Mendoza, Argentina, Gillies (?K, not seen).

*N. linifolia* var. *parviflora* Dun. in DC., Prodr. 13(1): 587. 1852. TYPE: Cordova, Argentina, Gillies (?K, not seen).

*Cyclostigma tenue* Phil., Sert. Mendoc. Alt. 39. 1871. TYPE: Mendoza, Chile (Argentina), Phillipi (G, W, neither seen; photos MO).

*Schwenckia tenuis* (Phil.) Griseb., Pl. Lorentz. 166. 1874.

*Salpiglossis linifolia* (Miers) Wettst. in Engl. & Prantl, Nat. Pflanzenfam. 4(3b): 36. 1891.

*Leptoglossis tenuis* (Phil.) Jackson, Ind. Kew. 2: 63. 1894 (1895), transfer incorrectly attributed to Bentham & Hooker.

*L. schwenkioides* var. *linifolia* (Miers) Monachino in Moldenke, Lilloa 5: 435. 1940.

*L. schwenkioides* var. *tenuis* (Phil.) Monachino in Moldenke, Lilloa 5: 435. 1940.

*Leptoglossis linifolia* is a small perennial reaching 12 cm tall. The leaves are smaller than in *L. schwenkioides*, although the pubescence is similar. The flowers are terminal, not forming differentiated panicles or racemes.

This species occurs in northwest Argentina.

The collection by Bruch-Carette cited below is a wiry plant of much sturdier construction than others; it may be taxonomically distinct.

ARGENTINA. Pampas Reise, Kuntze 16 Jan. 1892 (MO, NY). Pampas, W 34°, Kuntze 16 Jan. 1892 (NY). Banda oriental, Tweedie 1837 (K). BUENOS AIRES: Cañada de Lucas, Pampas B. Ayres, Gillies 835 (K). CÓRDOBA: Córdoba, Grisebach comm. 1878 (K). SAN JUAN: Río San Juan, Cuezco 1284 (TEX). SAN LUIS: Alto Pencoso, Bruch-Carette Feb. 1914 (NY). San Luis, Lorentz & Hieronymus 1873 (NY). Santa Rosa, 650 m, Varela 472 (NY). SANTIAGO DEL ESTERO: Loreto, Cuezco 2341 (TEX). Pinso, Kuntze Oct. 1892 (NY). Turena, Robles, Maldonado 254 (NY). Dept. La Banda, Dique Lod. Quirogas, Meyer 12804 (MO). TUCUMÁN: 5 km N de Tapia, Krapovikas et al. 27877 (MO). Chañar Pozo, 300 m, Venturi 5439 (A).

6b. ***Leptoglossis lomana*** (Diels) Hunziker, Kurtziana 10: 46. 1977.—FIG. 3B.

*Leptofeddea lomana* Diels, Repert. Spec. Nov. Regni Veg. 16: 193. 1919. TYPE: Peru, Weberbauer 1486 (B, if extant, not seen; photo MO).

- Salpiglossis linearis* Johnston, Contr. Gray Herb. 81: 96. 1928, non *S. linearis* Hook. 1831.  
 TYPE: Peru, *Pennell 13063* (GH, not seen; US, isotype).  
*S. albiflora* Johnston, Contr. Gray Herb. 85: 178. 1929. TYPE: Peru, *Weberbauer 7424a* (GH, MO, NY, US).  
*S. acutiloba* Johnston, Contr. Gray Herb. 85: 179. 1929, based on *Salpiglossis linearis* Johnston.  
*S. lomana* (Diels) Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(5b)(1): 143. 1962.

This species is an ephemeral herb attaining only ca. 15 cm. The leaves are oblanceolate, to 2 cm long, and on herbarium specimens, the rotund cotyledons are often persistent. The indumentum is of fine white hairs giving a greyish appearance. Flowers sometimes dry with a purplish or indigo cast.

*Leptoglossis lomana* occurs in sandy lomas and it ranges along most of the Peruvian coastal extent. There may be 2 species among the collections cited below which range from seaside to 2,600 m or higher.

PERU. AREQUIPA: 2 km S of Chala, 200 m, *Hutchison 1298* (F, NY). S of Mollendo, 15 m, *Mexia 04176* (MO), *7776* (F). Tiabaya, 2100–2200 m, *Pennell 13036* (NY, US), *Pennell 13081* (GH). Tingo, *Pennell 13119* (GH, NY). Jura, 2600 m, *Vargas 7984* (MO). CAJAMARCA: Portachuelo, 850 m, *Sagástegui et al. 7528* (MO). LIMA: Ambar, 2010 m, *Stork 11438* (GH). San Bartolomé, Lima-Oroyo railroad, 1500–1600 m, *Weberbauer 5297* (GH). MOQUEGUA: Mt. Estiquina NW of Moquegua, *Weberbauer 7424a* (GH, MO, NY, US).

- 6c. *Leptoglossis schwenkioides* Benth., Bot. Voy. Sulphur 143. 1844. TYPE: Peru, Barclay (K).—FIG. 3A.

*L. schwenkioides* var. *typica* Monachino in Moldenke, Lilloa 5: 435. 1940.  
*Salpiglossis schwenkioides* (Benth.) Wettst. in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 36. 1895.

This species is a shrub with numerous, entire, small or even scalelike leaves, reduced upwards. The flowers are numerous in the upper branches, subtended by small bracts and aggregated into poorly defined racemes and panicles. The calyces are more or less campanulate with 5 narrow lobes and evident membranous sinus areas. The corollas are cylindrical, mostly 1.0–1.5 cm long, and the tube is 1.0–1.5 mm wide. The throat tightly envelops the stamens and the limb is small.

*Leptoglossis schwenkioides* occurs in canyons above Lima.

PERU. LIMA: Lima, *Cumming 1010* (K). Above Sta. Eulalia, 1200 m, *Goodspeed 33098* (GH, MO). Canta Valley NE of Trapiche, *Hutchison 1032* (F, MO, NY). AMBAR: *Stork 11455* (GH). San Bartolomé, *Weberbauer 5290* (F, GH).

7. *Reyesia* Clos in Gay, Fl. Chil. 4: 418, tab. 52. 1849. TYPE: *R. chilensis* Clos.  
*Pteroglossis* Miers, Ann. Mag. Nat. Hist., ser. 2, 5: 32. 1850, non *Pteroglossa* Schlecht, 1920 (Orchidaceae). TYPE: *P. laxa* Miers = *Reyesia laxa* (Miers) D'Arcy.

Although *Reyesia* was recognized by Bentham & Hooker (1876), Wettstein's (1892, 1895) placing of this genus into *Salpiglossis* relegated it to obscurity until recently revived by Hunziker (1977). *Reyesia* is closely related to *Salpiglossis* as evidenced by its similar corolla shape and 2-armed stigma, but the didynamous stamens, sometimes pubescent filaments, and the persistent winged placenta in fruit are quite distinct. This winged placenta resembles that in *Lindernia*, Scrophulariaceae. An interesting feature is the pair of small wings on the style just below the stigma which is reported in *Reyesia chilensis* and in *Hunzikeria texana*. This is the lower half of a laminar style as is seen in *Leptoglossis* (Fig. 1C).

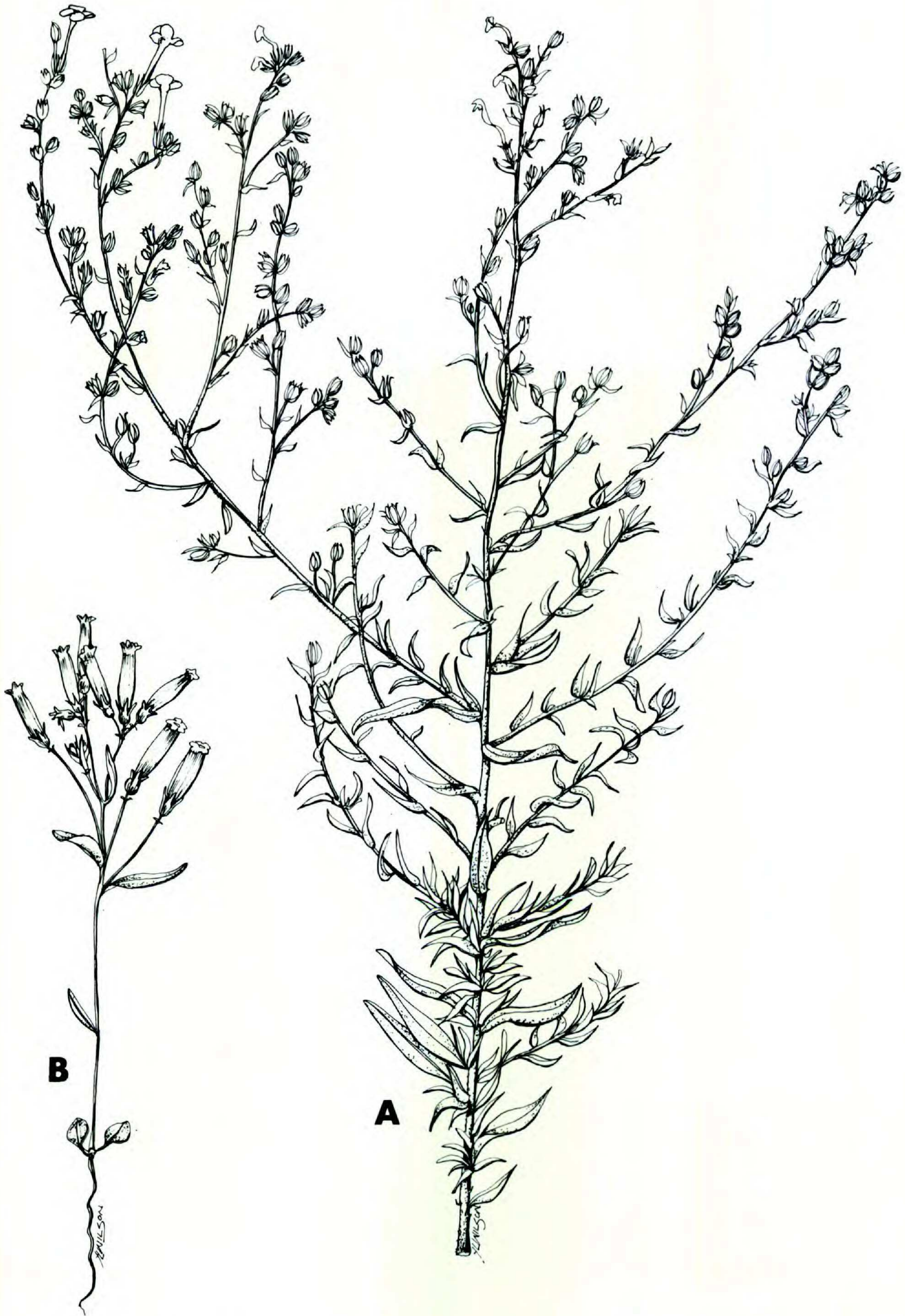


FIGURE 3. *Leptoglossis*.—A. *L. schwenckioides* Benth. Habit ( $\times\frac{3}{5}$ ). [After Hutchison 1032 (MO).]—B. *L. lomana* (Diels) Hunziker. Habit ( $\times 1\frac{1}{2}$ ). [After Mexia 04176 (MO).]

In the four species of *Reyesia* known to me, the corolla is minute, the stems slender and nearly leafless, and the lower leaves are sometimes undulate or lobed as in species of *Salpiglossis*. All species are from northern or central Chile.

7a. ***Reyesia cactorum*** (Johnston) D'Arcy, comb. nov.

*Salpiglossis cactorum* Johnston, Contr. Gray Herb. 85: 114. 1929. TYPE: Chile, *Johnston 5258* (US).

This species, which is from the same area as *Reyesia chilensis*, differs in having tomentulose stems, pilose petioles, bipinnatifid leaves and flowers to 15 mm long, twice as large as in *R. chilensis*. The corolla lobes appear to be rotate.

CHILE. Antofagasta, Dept. Taltal, near Aguada de Chardon, *Johnston 5258* (US).

7b. ***Reyesia chilensis*** Clos in Gay, Fl. Chil. 4: 418, *tab.* 52. 1849. TYPE: Chile, *Gay* (K, P, not dissected).—FIG. 1D.

*Salpiglossis chilensis* (Clos) Wettst. in Engl. & Prantl, Nat. Pflanzenfam. 4(3b): 36. 1895. *S. brachysiphon* Johnston, Contr. Gray Herb. 85: 161. 1929. TYPE: Chile, Antofagasta, hills near Tocopilla, *Johnston 3625* (GH, not seen).

Much-branched *perennial* from a woody base; stems wiry, puberulent. *Basal leaves* oblanceolate, 4–5 cm long, 5 mm wide, shallowly lobed or entire, the costa prominent beneath, narrowed to an elongate petiole, glabrate; *cauline leaves* mostly reduced to linear scales. *Inflorescence* of scattered terminal or subterminal flowers; pedicels filiform, apically glandular, subtended by scalelike bracts. *Flowers* 6–7 mm long, narrow; calyx 5-lobed, 2 mm long, campanulate or slightly urceolate, the lobes acute, the costas continuous from the tube, contrasting with the sinus areas; corolla white, drying conspicuously bluish-nervate, the tube expanding gradually, the limb campanulate, short-lobed; stamens 4, didynamous, the filaments pubescent; style apically winged, the stigma 2-armed. *Capsule* 4-valved, the valves about equalling the calyx lobes; seeds minute.

In spite of the size and branching difference noted by Johnston, the type of *Salpiglossis brachysiphon* is well within the variation of other material seen of *Reyesia chilensis*.

This species is notable for its numerous, nearly leafless wiry stems and minute flowers. It occurs in central Chile.

CHILE. ANTOFAGASTA: Tocopilla, *Jaffuel 1003* (GH); *Johnston 3625* (GH). Hills SE of Taltal, *Johnston 5084* (GH). Taltal, *Johnston 5650* (GH). 5 km SE of Taltal, 200 m, *Morrison 17095* (MO). Taltal, 100 m, *Werdermann 821* (MO, NY). ATACAMÁ: Desert of Atacamá, *Geisse 170* (NY). Alto del Carmen, Vallenar, 800 m, *Werdermann 156* (GH, MO). 3 km SW of Huasco, *Worth & Morrison 16243* (GH). COQUIMBO: Tres Cruces, Serena, *Muñoz 325* (GH).

7c. ***Reyesia juniperoides*** (Werderm.) D'Arcy, comb. nov.

*Salpiglossis* (*Reyesia*) *juniperoides* Werderm., Notizbl. Bot. Gart. Berlin 10: 474. 1928. TYPE: Chile, *Werdermann 1054* (B, if extant, not seen; F, GH, MO, NY, US, isotypes).

Robust, profusely branched glabrate *shrub*; stems slender, rigidly woody, the internodes short, appearing leafless. *Cauline leaves* reduced to sublinear, cuculate scales to 1 mm long. *Flowers* solitary, scattered on the upper branches; calyx

narrow, 5-lobed about halfway down; corolla ca. 7 mm long, the tube narrowly ascending upwards, the throat small, differentiated, the limb ellipsoidal in bud; stamens 4, didynamous; stigma 2-armed. *Capsule* indurate, stramineous, 2- or 4-valved, the placenta peglike, winged by the broad dissepiment.

*Reyesia juniperoides* is superficially much like *R. chilensis*, but the branching is much sturdier, subspinose, and the corolla tube is relatively longer and narrower. It is known only from central Chile.

CHILE: Tarapaca, Cordillera Quebrada de Quipisca, Palca, 2500 m, *Werdermann 1054* (F, GH, MO, NY, US).

7d. ***Reyesia laxa*** (Miers) D'Arcy, comb. nov.

*Pteroglossis laxa* Miers, Ann. Mag. Nat. Hist., ser. 2, 5: 33. 1850; Ill. S. Amer. Pl. 2: 62, *tab.* 52. 1857. TYPE: Coquimbo, *Bridges 1839* (K, not seen).

*Salpiglossis parviflora* Phil., Viaj. Des. Atacamá 219. 1860. TYPE: Coquimbo, Chile, *Philippi* (SGO, not seen; photo (poor) GH; dupla B if extant, photo MO).

*Reyesia parviflora* (Phil.) Hunziker, Kurtziana 10: 46. 1977.

In this species the stems are less wiry and less intricately branched than in the preceding species. The basal leaves are obovate, crenately lobed, 3–5 cm long forming a rosette. The corolla, ca. 8 mm long, has a broader tube and the throat is less differentiated.

*Reyesia laxa* is known only from the hillsides of central Chile and adjacent Argentina (San Juan Province).

ARGENTINA. SAN JUAN: Near Baños San Crespín, 3300 m, *Johnston 6115* (GH). Río de la Tagua below junction with Río de la Sal, 2900 m, *Johnston 6146* (GH).

CHILE. Baños del Toro, 3500 m, *Werdermann 195* (GH, MO). ATACAMÁ: Molle, *Geisse 1889–1890* (GH). Quebrada de Doña Ines, Chañaral, *Gigoux 1886* (GH). Potrerillos, 2800 m, *Johnston 4743* (GH). COQUIMBO: Río Toro above Los Baños, 3300 m, *Morrison 17266* (GH, MO). Río Seco, 14 km E of Nueva Elqui, *Wagenknecht 18119* (MO). 98 km from Rivadavia to Laguna Dam, 2900 m, *Worth & Morrison 16399*.

8. ***Nierembergia*** Ruiz & Pavón, Fl. Peruv. Chil. Prodr. 23. 1794. TYPE: *N. repens* Ruiz & Pavón.

*Nierembergia* embraces about 35 species of Argentina and Chile with 1 species disjunct in Mexico. The genus was revised by Millán (1940, 1941). In *Nierembergia* the corolla is salverform as in *Hunzikeria*, but the androecium consists of 5 similar stamens with filaments inserted at various levels but united at least in part to form a tube surrounding the style. The stigma is generally enlarged into a 2-armed or crescent-shaped process between or surmounting the anthers. Di Fulvio (1975b) reported that the pollen of some species is in tetrads. Only the Mexican species, *N. angustifolia*, is discussed here.

8a. ***Nierembergia angustifolia*** H.B.K., Nov. Gen. Sp. Pl. 3: 9, *tab.* 198. 1818. TYPE: Mexico, Real del Monte (not seen).—FIGS. 1F, 4.

*Bouchetia procumbens* DC. ex Dun. in DC., Prodr. 13(1): 389. 1852, based on Moçino & Sessé *plate 920* (G).

This species differs from most other species discussed in this paper in being



almost completely glabrous. It is widespread in Mexico, but collections are few. The corolla appears on the herbarium sheet much like that of *Hunzikeria texana*, but the androecium and gynoecium are quite different. The filaments in this species are connate below and free above, the united portion forming a short tube which is open along one side. The anthers are alike but differ in size and are situated in two groups, one slightly above the other. In this species the style arms are less developed than in many South American species, but they are present, contrary to observations of Millán.

For a discussion of the typification of *Bouchetia procumbens* and further notes on the morphology of this plant, see under *Salpiglossis*, below.

MEXICO. DURANGO: Near Durango, *Palmer 121* (C, F, MO). MEXICO: Laguna de Atenco, 2250 m, *Rzedowski 22072* (MSC, TEX). MICHOACÁN: Near Morelia, *Pringle 4149* (F, KM, MSC, MO). PUEBLA: Laguna San Baltasar near Puebla, 2135 m, *Arsène 292* (MO). SAN LUIS POTOSÍ: Near San Luis Potosí, *Parry & Palmer 630* (BM, F, K, MO). WITHOUT LOCALITY: Ex herb. *Sessé & Moçino* (F).

9. **Salpiglossis** Ruiz & Pavón, Fl. Peruv. Chil. Prodr. 94, *tab. 19*. 1794. TYPE: *S. sinuata* Ruiz & Pavón.—FIG. 1E.

*Bouchetia* DC. ex Dunal in DC., Prodr. 13(1): 589. 1852. TYPE: *B. erecta* Dun. = *Salpiglossis erecta* (Dun.) D'Arcy.

*Salpiglossis sinuata* is a large-flowered species from central Chile which is frequently cultivated in temperate gardens for its showy flowers. This species grows to 1 m tall and may have flowers as large as 6 cm across. The upper leaves are entire but lower leaves may be sinuate. This species characterizes the genus *Salpiglossis* as having campanulate, often strongly nerved corollas, 4(5) similar stamens inserted low in the corolla tube and sometimes a staminode, and a somewhat expanded, 2-armed stigma grooved as if to accommodate the anthers at some earlier stage of growth or evolution. Sometimes one or more stamens is reduced but not in a definite pattern of didynamy as in some related genera. Traditionally *Salpiglossis* has included large-flowered horticultural plants and a heterogenous assembly of small-flowered plants, many of which belong to other genera. Wettstein (1895) placed elements of *Reyesia* and *Leptoglossis* in *Salpiglossis* and this has been followed by many workers, including Werdermann (1928) who treated the genus for Chile. I remove discordant elements from *Salpiglossis* and bring plants hitherto known as *Bouchetia* into *Salpiglossis*.

*Typification of Bouchetia.*—*Bouchetia* is here placed into synonymy under *Salpiglossis*, but because of its long use for plants in both North and South America, a discussion of its typification is in order. The name *Bouchetia* honors Dominique Bouchet-Doumeng, an amateur botanist of Montpellier, who was born near Avignon in 1770 and died at Montpellier in 1845. *Bouchetia* was first described in the Solanaceae in de Candolle's *Prodromus* (1852) with two species, *B. procumbens* and *B. erecta*. The Solanaceae treatment of the *Prodromus* was written by M. F. Dunal of Montpellier, one of de Candolle's students. Although the names are generally attributed to de Candolle, Stafleu & Cowan (1976: 290) and the *Index Nominum Genericorum* cite Dunal as the author. Dunal himself attributed the treatment of *Bouchetia* in the *Prodromus* to de Candolle "DC. mss."

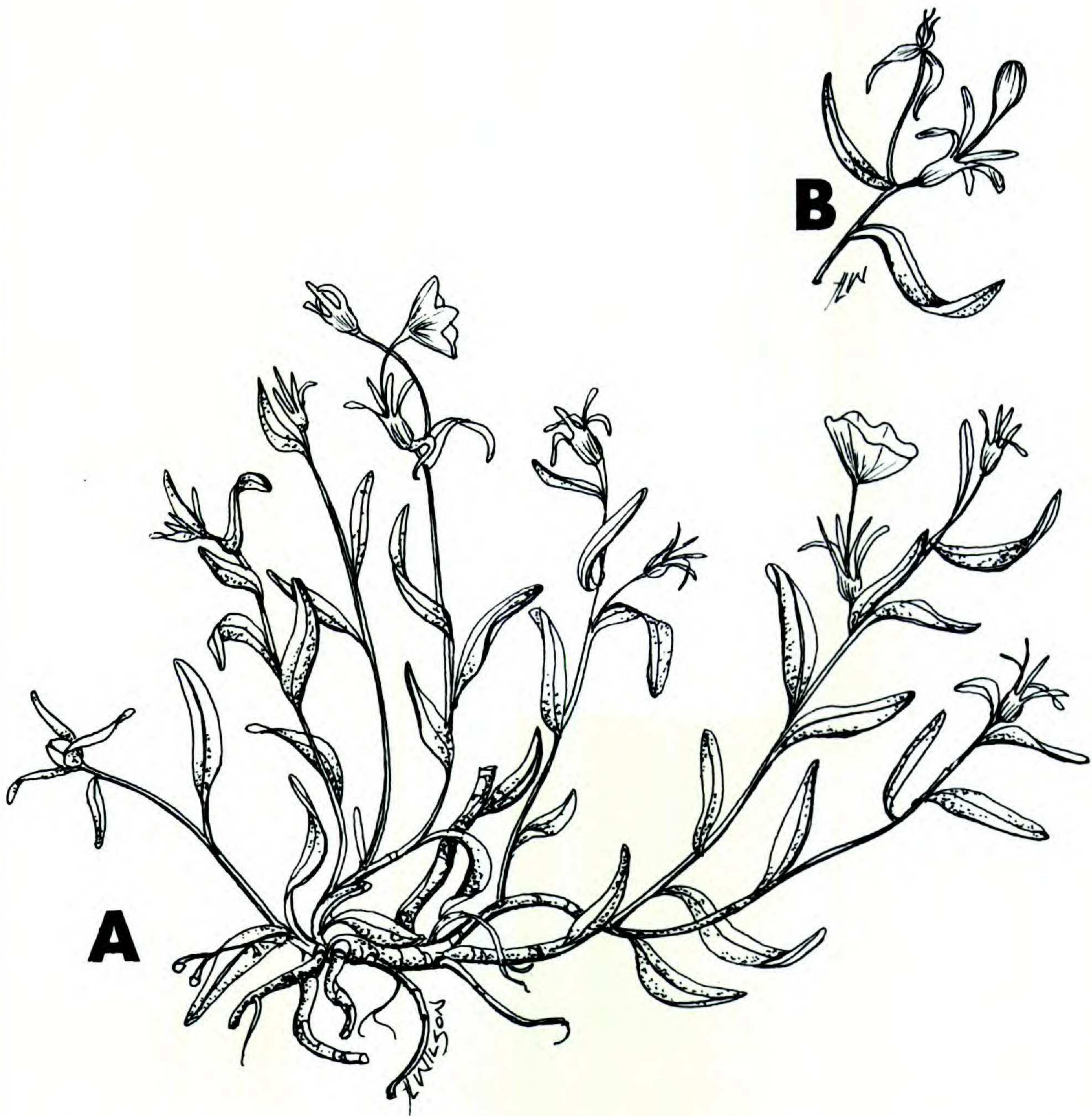


FIGURE 4. *Nierembergia angustifolia* H. B. K.—A. Habit ( $\times 2$ ).—B. Flower bud ( $1\frac{1}{2}$ ). [After Palmer 121 (MO).]

Although a number of elements are cited under the original description of *Bouchetia* and its two species, only material available to August Pyramus de Candolle is directly relevant for typification. Under *B. procumbens*, only plate no. 920 of Moçino & Sessé is cited. Under *B. erecta*, plate no. 921 of Moçino & Sessé is cited as well as several other elements including some specimens. These plates are part of a series of colored illustrations of Mexican plants brought by José Mariano Moçino to Montpellier in 1815 when he fled Spain for political reasons. De Candolle and his student Dunal studied these plates and de Candolle was able to obtain part of the corresponding text which had been seized in Spain and stored in a cave in Paris (A. P. de Candolle, 1862). Some of the plates were copied in Montpellier by Node Vèran, a noted artist of the time who also prepared the plates for Dunal's thesis on the Solanaceae. In 1816 de Candolle left Mont-

pellier for Geneva and at the urging of Moçino, who was in failing health, took the plates with him. Shortly after de Candolle's installation at Geneva, Moçino had a change of heart and demanded the plates back. De Candolle hurriedly assembled a group of townspeople to copy the remaining plates before the originals were returned. The product is of variable quality, some of the copies being fine, colored works and probably close renditions of the originals, while others are crude, and many are unfinished. The copies are now in Geneva, but the originals returned to Moçino have since disappeared. In 1874, Alphonse de Candolle, the son who was editor of the final volumes of the *Prodromus*, had tracings made of the Geneva copies and distributed them as the *Calques des Dessins* (A. L. P. P. de Candolle, 1874). This convoluted history of the Sessé-Moçino plates is significant to typification of *Bouchetia*.

The two Moçino & Sessé copies cited under *Bouchetia* agree well with the diagnoses, but the amplified description of *B. erecta* includes details which are not evident on the copies, e.g., caules puberuli, folia ciliata, pedunculus pubescenti-hirsutus. These details may have been present on the Moçino originals or gleaned from the corresponding text, or they may have been added by Dunal from the specimens he cited.

The first element cited under *Bouchetia erecta* is a specimen in the de Candolle herbarium collected in Texas by Wright. Charles Wright collected in Texas in 1849 and a set of duplicates was personally delivered by Asa Gray to Alphonse de Candolle on a visit of 1850 (McKelvey, 1955). This was much too late for study by Augustin de Candolle, who died in 1841, but was probably not too late for study by Dunal before completing the Solanaceae treatment for the *Prodromus*. The Wright collection in the de Candolle herbarium is a mixture, the left-hand specimen corresponding to the diagnoses of *Bouchetia* and the right-hand specimen being a plant of *Hunzikeria texana*. The mixing was probably of Gray's doing, for he generally ignored Wright's field numbers and assembled similar plants into sets for sale (McKelvey, 1955).

Also cited under *B. erecta* is a crude, highly stylized drawing of three erect, narrow-leaved stems with a thick root referred to as *Itzticapitli* in Francisco Hernandez's 1651 volume on Mexican medicinal plants. Although it bears little resemblance to the plants now identified with *Bouchetia*, this drawing is not unlike the Geneva copy of *Bouchetia erecta*, plate no. 921. In fact, the roots of the two plates are so much alike that I suspect that de Candolle's local artist looked to the Hernandez plate for assistance in copying the Moçino illustration.

Another specimen cited is a plant in the general herbarium at Geneva labeled *Maleolaria lanceolata* Pav., ex herb. Pav. This also corresponds to the *Bouchetia* diagnosis and appears to be the same species as the left-hand Wright collection. Finally, specimens cited as *Nierembergia* of the Wright herbarium have not been located.

The type of *Bouchetia erecta* is the Geneva copy of Moçino & Sessé plate no. 921 which represents a species of Solanaceae found in Mexico and Texas and perhaps in Argentina. Although I have seen no herbarium material with the large roots illustrated, they may well be present on entire plants. This species is here chosen as lectotype of the genus *Bouchetia*. Before submitting de Candolle's

first manuscript for inclusion in the *Prodromus*, Dunal was able to review actual specimens which helped confirm his acceptance of de Candolle's concept of *B. erecta*; no such review was possible for *B. procumbens*. This selection of lectotype maintains the concept of *Bouchetia* which subsequent authors have accepted. To choose *B. procumbens* as lectotype would break this tradition, as is outlined below.

Since the first description of *Bouchetia procumbens*, there have been discordant attempts to relate plate 920 to later collections. Bentham & Hooker (1876) identified the plate with two Mexican collections, *Galeotti 1476* and *Bourgeau 68* and referred them to *Nierembergia*. Soon after, Hemsley (1881) disagreed and related the name *Bouchetia procumbens* to a different series of Mexican plants. He noted that in *Bouchetia* the corolla tube tapers gradually and the stamens are free, inserted low in the corolla. Robinson (1904) reviewed some of the specimens cited by Hemsley and refused to accept them as the same species as plate 920. In this paper he described *Bouchetia arniatera* based on material cited by Hemsley and new material he had seen. Both Hemsley and Robinson based their concepts of *Bouchetia procumbens* on the Calques des Dessins copy of plate 920 and not on the copy in Geneva. Although agreeing in most details, the tracing copy differs notably from the Geneva copy in its poor rendition of flower buds which in this case are diagnostic.

With more material at hand and a view of both extant copies of plate 920, I must concur with Hooker and Robinson and relate *B. procumbens* to *Nierembergia* and not to *Bouchetia* as typified by *B. erecta*. *Nierembergia angustifolia* H.B.K. grows in Mexico and agrees with the plate in most features, especially in the following: leaves narrow, slightly broader above the middle, the flowers distributed along the branches rather than mostly terminal (as in *Bouchetia*), the calyx divided halfway or more with the lobes pointed and spreading, the corolla tube remaining narrow until well out of the tube, and pointed corolla lobes. The detailed drawings on plate 920 show 5 stamens inserted just above the top of the tube. And most important, the corolla buds (see Fig. 4B) consist of a slender, exerted tube with the unexpanded limb forming a subglobose or elliptic knob whereas in *Bouchetia* the exposed portion of the corolla in bud consists of a narrowly elliptic truncate limb, and the narrow portion of the tube is concealed by the calyx. The type of *Bouchetia procumbens* is the Geneva copy of Moçino & Sessé plate 920 which is a representation of *Nierembergia angustifolia* H.B.K. It is of interest that a collection of *Nierembergia angustifolia* is among the specimens from the Sessé & Moçino herbarium now at the Field Museum, Chicago.

The full citation for these names is *Bouchetia* DC. ex Dunal in DC. But to follow common practice, this may be shortened to *Bouchetia* Dunal in DC., or to *Bouchetia* Dun.

9a. **Salpiglossis anomala** (Miers) D'Arcy, comb. nov.

*Nierembergia anomala* Miers, London J. Bot. 5: 175. 1846. TYPE: Argentina, Cordoba, Miers (K).

?*N. staticifolia* Sendt. in Mart., Fl. Bras. 10: 179. 1 July 1846. TYPE: Brasil, Sello (B, if extant, not seen; photos C, MO).

*Bouchetia anomala* (Miers) Loes., Bot. Jahrb. Syst. 29: 105. 1901.

*B. anomala* (Miers) Britt. & Rusby, Trans. New York Acad. Sci. 7: 12. 1887, redundant combination.

?*B. anomala* subsp. *staticifolia* (Sendt.) Loes., Bot. Jahrb. Syst. 29: 106. 1900.

*Nierembergia miersiana* Sendt. in Mart., Fl. Bras. 10(1): 200 in obs. nomen nudum.

?*Petunia staticifolia* (Sendt.) O. Kuntze, Rev. Gen. Pl. 3(2): 223. 1898, in syn.

?*Nicotiana staticifolia* (Sendt.) O. Kuntze, Rev. Gen. Pl. 3(2): 223. 1898.

The photograph of the Sello collection which supports *Nierembergia staticifolia* appears to represent the same species as *Nierembergia anomala*, but it must be remembered that the synonymy effected here is based only on the photograph and a limited range of Argentinian material.

*Salpiglossis anomala* is quite similar to plants of North America treated here as *S. erecta*, but the pubescence is glandular and the calyx displays a more membranous area in the sinuses than the North American plants.

ARGENTINA. CHACO: *Schulz* 7423 (C). CÓRDOBA: *Lossen* 224 (F, MO); *Tweedie* 1122 (K). CORRIENTES: *Pedersen* 849, 9269 (both C). ENTRE RÍOS: *Huidobro* 3474 (MO), 3426 (G). FORMOSA: *Jørgensen* 2991 (MO); *Morel* 5 (G); *Pederson* 1268 (C). MISSIONES: Posadas, *Ekman* 863 (G). SALTA: *Romero* 21 Jan. 1947 (C). TUCUMÁN: El Puestito, *Venturi* 7355 (MO).

9b. ***Salpiglossis arniatera*** (Robinson) D'Arcy, comb. nov.—FIG. 5B.

*Bouchetia arniatera* Robinson, Bot. Gaz. (Crawfordsville) 38: 377. 1904. TYPE: Mexico, *Dugès* (GH, not seen; K, MINN, isotypes).

This species differs from the other Mexican species, *S. erecta*, in having a much longer corolla tube, which while it expands is still quite narrow until well beyond the calyx lobes. This corolla, apparently definitely purplish, is 2–3 cm long and opens to nearly 2 cm across. The calyx is larger than that of *S. erecta* and is proportionally more deeply lobed than other species of *Salpiglossis*. The plants are diminutive, less than 10 cm long, several stems arising from a woody rootstock.

*Salpiglossis arniatera* has been collected from widely scattered points in Mexico, mainly from the uplands. Its range is generally to the south and west of *S. erecta*. Across its range, the species shows some variation but this is difficult to ascertain from the few specimens available. It was first brought to scientific attention because it was reputed to poison sheep.

MEXICO. COAHUILA: 24 km NW of Fraile, 2350 m, *Stanford et al.* 432 (MO). DISTRITO FEDERAL: Lomas, *Lyonnet* 660 (K, MO). DURANGO: Vicinity of Rancho Ojito, *Correll & Johnston* 21466 (TEX). MICHOACÁN: W of Morelia, *Gregg* 787 (MO). NUEVO LEÓN: Cieneguillas to Pabullo, *Mueller & Mueller* 870 (F, TEX). Hacienda Pabullo, Galeana, *Taylor* 18 (F, MO), 74 (F, K, TEX). SAN LUIS POTOSÍ: Region of San Luis Potosí, *Parry & Palmer* 701 (K, MO, US); *Schattner* 1826 (K). TAMAULIPAS: *Stanford et al.* 2603 (GH). VERACRUZ: Jalapa, *Graham* 270 (K). ZACATECAS: Hacienda de Santiago, *Dugès* 1904 (K, MINN).

9c. ***Salpiglossis erecta*** (Dun.) D'Arcy, comb. nov.—FIGS. 1E, 5A.

*Bouchetia erecta* DC. ex Dun. in DC., Prodr. 13(1): 589. 1852, based on Moçino & Sessé plate 921 (G).

*Maleolaria lanceolata* DC. ex Dun. in DC., Prodr. 13(1): 589. 1852, in syn. nom. nud. TYPE: *Pavón* (G).

*Leucantha roemeriana* Scheele, Linnaea 25: 259. 1852 (1853). TYPE: Texas, *Roemer* (B).

*Nierembergia anomala* var. *uniflora* Dun. in DC., Prodr. 13(1): 588. 1852. LECTOTYPE: Texas, *Drummond* 245 (G-DC).

*Bouchetia anomala* sensu Britt. & Rusby, Trans. New York Acad. Sci. 7: 12. 1887, non Miers. *Bouchetia anomala* subsp. *erecta* (DC.) Loes., Bot. Jahrb. Syst. 29: 105. 1900.

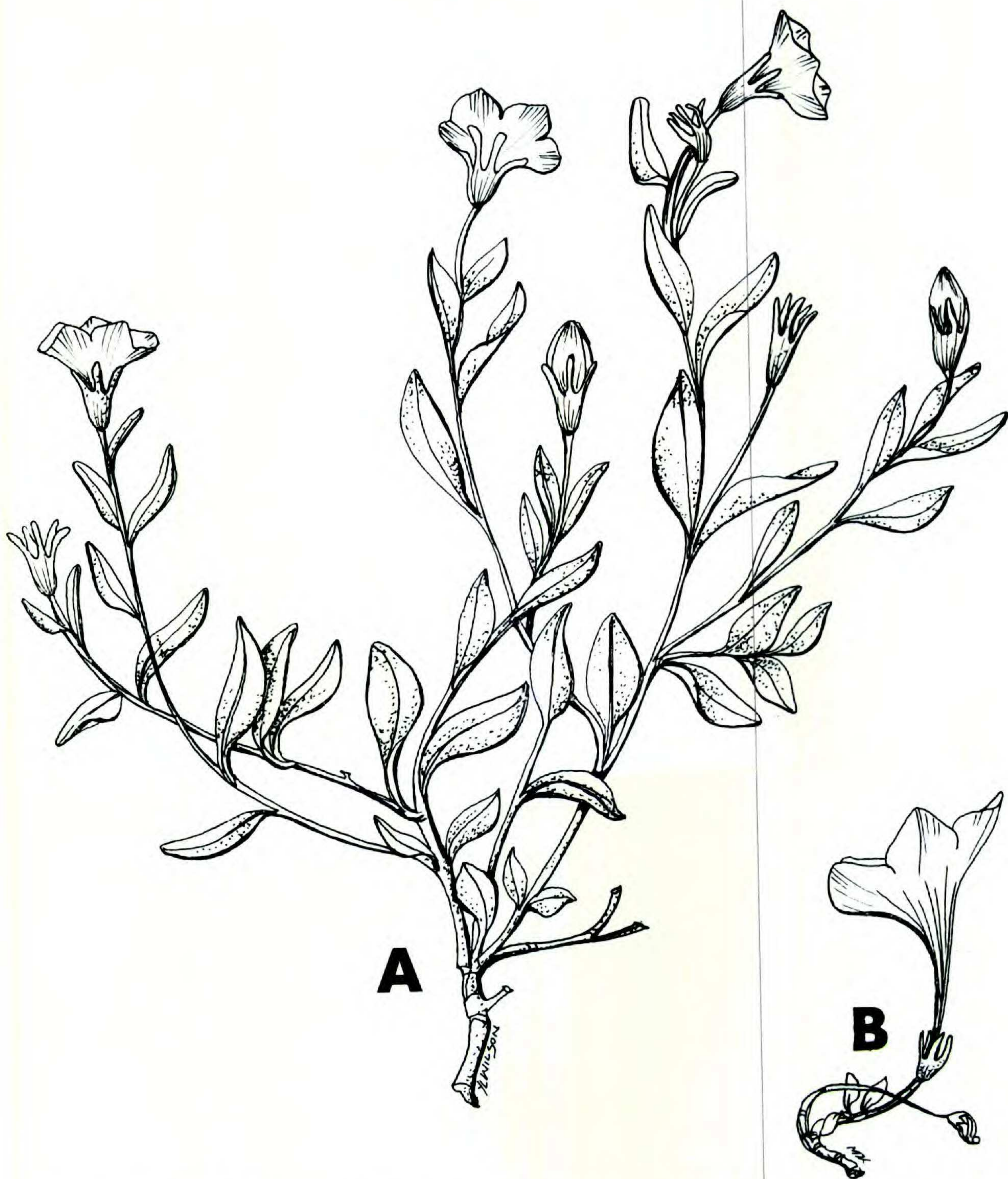


FIGURE 5. *Salpiglossis*.—A. *S. erecta* (Dun.) D'Arcy. Habit ( $\times \frac{9}{10}$ ). [After Palmer 12124 (MO).]—B. *S. arniatera* (Robinson) D'Arcy. Flower ( $\times 1\frac{2}{5}$ ). [After Parry & Palmer 701 (MO).]

Diminutive *perennial* from a woody root, to 20 cm tall; stems flexuous, pubescent with short, white, appressed ascending hairs. *Leaves* elliptical, often narrowly so, mostly slightly wider above the middle, mostly 10–20 mm long, 4–7 mm wide, apically acute, sometimes minutely callose, costate, the lateral venation obscure, both sides minutely pubescent with appressed hairs, more so beneath; petiole to 5 mm long or obsolete. *Inflorescences* solitary or paired terminal flowers; pedicels to 3 cm long, subtended by normal leaves. *Flowers* with the calyx campanulate, 7–12 mm long, lobed ca.  $\frac{1}{4}$  way down, the lobes

narrow, blunt, the tube 10-nerved, the sinus areas little differentiated, not accrescent; corolla mostly white, funnelform, to ca. 20 mm long, the tube included in the calyx, the limb campanulate to obconical, mostly exserted, becoming 10 mm across, shallowly lobed; stamens 4–5, one or more anther thecae sometimes reduced, inserted in the bottom half of the corolla tube; stigma 2-armed, slightly exceeding the anthers. *Capsule* 4-valved, slightly emergent from the calyx tube; seeds numerous, minute, prismatic.

*Salpiglossis erecta* ranges from Texas to Guatemala (Gentry & Standley, 1974). It has been collected from a wide range of open habitats. This species may not be distinct from *S. anomala* of Argentina, in which case the name *S. anomala* should be applied to the North American plants. There do appear to be differences between plants on the two continents, and careful study will be needed to assess the importance of these differences. *Salpiglossis erecta* was illustrated (as *Bouchetia*) by Gentry & Standley (1974).

UNITED STATES. TEXAS: San Antonio, *Bush* 1184 (MO); *Clemens & Clemens* 251 (F, MO), 249 (MO). 1½ mi NE of Vidauri, Refugio Co., *Correll* 14822 (TEX). 9 mi W of Tivoli, Refugio Co., *Correll* 27015 (TEX). 7.5 mi W of D'Hanis, Medina Co., *Correll & Rollins* 32521 (TEX). 4 mi S of Marble Falls, Burnet Co., *Correll et al.* 15902 (TEX). Seadrift, Calhoun Co., *Cory* 49074 (TEX). San Filipo, *Drummond* 245 (G, K). Near San Antonio, *Eggert* 4 April 1905 (MO). Near Bracken, *Groth* 81 (F). Austin, *Hall* 383 (F, MO). San Antonio, *Havard* 12 (F). Gillespie Co., herb. *Gustav Jeremy* (MO). 13 mi N of San Antonio, Becar Co., *Johnston* 2389 (TEX). 4.2 mi from Travis Co. line on Highway 183, Williamson Co., *Johnston & McCart* 5256 (TEX). 5 mi S of Blanco, Blanco Co., *Johnston & Webster* 509 (TEX). Without other locality, *Lindheimer* 471 (276) (F, K, MO). Comanche Springs, *Lindheimer* 1034 (189) (BM, C, G, MO, TEX). New Braunfels, *Lindheimer* 1035 (346) (C, F, K, M, MO, TEX). Without other locality, *Neally* 1893 (MO). Uvalde, *Palmer* 11041 (MO). Sabinal, *Palmer* 11518 (MO). San Marcos, *Palmer* 12124 (MO). Near San Saba, *Reverchon* 1567 (F, MO). Yorktown, *Riedel* 1942 (MO). 4 mi NW of Sinton, San Patricio Co., *Rogers* 6648 (TEX). Harthaven, Travis Co., *Warnock* W1007 (TEX). New Braunfels, Comal Co., *Warnock* 46257 (TEX). Zilker Park, Travis Co., *Webster* 61 (TEX). Without other locality, *Wright* (G-DC, left-hand specimen, MPU). Travis University Campus, Austin, *Young* 1913 (MO, TEX).

MEXICO. COAHUILA: Lerios, 10,000 ft, *Palmer* 852 (F). HIDALGO: Near Jacala, *Edwards* 763 (F). Hills above Pachuca, 8500 ft, *Pringle* (BM, F, G, K, MO, MSC). MÉXICO: 20 km NE of Texcoco, 2850 m, *Cisneros* (MSC). 5 km N of Atizapán, 2350 m, *Rzedowski* 20881 (MSC). MICHOACÁN: Near Morelia, *Arsène* 5595 (MO). MORELIA: Punguato, *Arsène* 52b (F). NUEVO LEÓN: 12 mi E of Monterrey, *Barkley* 14368 (TEX). Nuevo León, *Lacas* 325 (F). Santiago, 2300 ft, *Leavenworth* 124 (F). 18 km S of Monterrey, *Marroquin* 1339 (TEX). Monterrey, *Mueller & Mueller* 290 (TEX). 15 mi SW of Pueblo Galeana, 7500–8000 ft, *Mueller & Mueller* 334 (TEX). Road up Chipinque, *Webster & Aquirre* 2951 (TEX). PUEBLA: Esperanza, *Purpus* 2494 (BM, F, G, MO). Near San Luis Tultitlanapa, *Purpus* 3265 (MO). SAN LUIS POTOSÍ: 30 mi E of San Luis Potosí, 6900 ft, *McGregor et al.* 577 (TEX). Minas de San Rafael, *Purpus* 5350 (F, MO).

9d. *Salpiglossis sinuata* Ruiz & Pavón, Syst. Veg. 163. 1798. TYPE: Peru, *Ruiz*, not seen.

*S. straminea* Hook., Exot. Fl. 3, tab. 229. 1823.

*S. picta* Sweet, Brit. Flower Gard., ser. 1, tab. 258. 1826.

*S. atro-purpurea* R. Graham, Edinburgh New Philos. J. 1827 (Oct.–Dec.): 176. 1827. TYPE: not seen. Based on plants cultivated in Scotland from seed received from Gillies, collected on hills 50 mi beyond (W of) Mendoza.

*S. intermedia* Sweet, Hort. Brit., ed. 2: 594. 1830; Brit. Flower Gard., ser. 2, tab. 112. 1831. Based on a plant cultivated in England.

*S. barclayana* Sweet, Brit. Flower Gard., ser. 2, tab. 112. 1833. Based on a plant cultivated in England.

*S. barcklayana* Penny ex G. Don., Loud, Hort. Brit. Suppl. 1: 599. 1850 (not seen).

- S. coccinea* Lindl. & Paxt., Flow. Gard. 3: 135, *tab. 100*. 1852–1853.  
*S. aurea* Hort. ex Vilm., Fl. Pl. Terre, ed. 1: 762. 1863 (not seen).  
*S. hybrida* Vilm., Fl. Pl. Terre, ed. 1: 767. 1863 (not seen).  
*S. variabilis* Vilm., Fl. Pl. Terre, ed. 2: 809. 1866 (not seen), nom. nud. Based on a plant cultivated in France.

This species is widely cultivated in north temperate gardens. This and *S. spinescens* are the only large-flowered species in the genus. It is quite variable in flower color suggesting more than one taxonomic element may be present.

CHILE. Cordilleras, *Cuming's Herb.* 246, 294, 371, 445 (all GH). Without other locality, *Gay* 204 (GH, NY). Pajo Cruz, 1500 m, *Kuntze* 192 (NY). Andes, Capt. *Reynolds* (GH). ACONAGUA: 3 km E of Río Blanco, 1700 m, *Hutchinson* 175 (GH). Ca. 15 km E of Melón, 1700 m, *Morrison* 16856 (GH, MO). 18 km E of La Ligua, 1900–2200 m, *Morrison* 17067 (MO). Riecillo, 1400 m, *Zöllner* 8391 (MO). COLCHAGUA: Near Quinta and Taguatagua, *Bertero* 1289 (?599) (NY). Centinela, San Fernando, *Montero* 20 (GH). CURICÓ: Los Quenes, Andes de Curicó, 1000 m, *Aravena* 33374 (GH, MO). Hacienda Monte Grande, 1600 m, *Werdermann* 506 (GH, MO, NY). MALLECO: Ercilla, *Kuntze II* 192 (NY). MAULE: Near Cauguenes, *Reid* (NY). O'HIGGINS: Copada, *Pennell* 12236 (NY). SANTIAGO: Prope Tiltill, 1400 m, *Grandjot* x31, x32 (both MO). Cerro Provincia, Cordillera de Santiago, 1600 m, *Grandjot* xi1932, 3637 (GH). Santiago, 1400 m, *Montero* 312 (GH, MO). Cumbra de la Dormida, *Senn* 4527 (MO). VALPARAÍSO: Valparaíso, *Bertero* 1290 (NY). Concón, *Miers* (MO). Las Viscachas, 10 km from La Dormida, 1700–1900 m, *Morrison* 16747 (GH). Ca. 12 km from Valparaíso, 50–60 m, *Morrison* 16835 (GH, MO). Prope Concón, *Poeppig* 163 (GH, MO).

PERU. Perou, *Dombey* (NY).

- 9e. *Salpiglossis spinescens* Clos in *Gay*, Fl. Chil. 5: 127. 1849. TYPE: Chile, Copaiipo, *Gay* Feb. 1843 (G, not seen; photo MO).

This is a large flowered species with corollas to 4 cm long. The plants are densely glandular-pilose and some shoots are indurated into spinelike processes. A shrub approaching a meter in stature, the stems are devoid of normally developed leaves. Clos reported that it occurs in Coquimbo as well as in Atacamá. *Werdermann* (1928) found it only in Copaiipo.

CHILE. ATACAMÁ: Desert of Atacamá, *Geisse* 16 (NY). Below Agua Dulce, Quebrada de Potrerillos, 2500 m, *Johnston* 3683 (GH). Tierra amarilla, dept. Copaiipo, 700 m, *Werdermann* 419 (GH, MO, NY).

#### EXCLUDED NAMES

A number of names published in *Salpiglossis* have been noted under other genera in this paper. Several names must be excluded:

- Salpiglossis fulva* Court., Amer. Gard. Mag. 1: 219, n. 411. 1835.  
*S. integrifolia* Lodd., Bot. Cab. *tab. 1978*. 1833. = *Petunia* sp. TYPE: Cultivated in Scotland from seed received from Buenos Aires (not seen).  
*S. integrifolia* Hook., Bot. Mag. *tab. 3113*. 1831. = ?*Petunia violacea* Lindl.  
*Petunia integrifolia* (Hook.) Schinz & Thell., Vierteljahrschr. Naturf. Ges. Zürich 60: 361. 1915; *Nicotiana integrifolia* (Hook.) O. Kuntze.  
*S. linearis* Hook., Bot. Mag. sub *tab. 3113*. 1831. = *Petunia linearis* (Hook.) Paxt.  
*S. parviflora* G. Don. ex Benth. in DC., Prodr. 10: 202. 1846, nom. nud. = ?  
*S. prostrata* Hook. & Arn., Bot. Beech Voy. 153. 1841. = *Petunia parviflora* Juss., fide *Fries* 1911. TYPE: California (?K, not seen).  
*S. purpurea* Miers, Trav. 2: 531. 1826, nom. nud.



*S. sinuata* Hook. & Arn. ex Miers, London J. Bot. 5: 190. 1846, nom. nud., non Ruiz & Pavón = *Petunia parviflora* Juss., fide Fries 1911.

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